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From cooperation between Max-Planck-Institute for Limnology, Department of Tropical Ecology, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus-Amazonas, Brazil

Da cooperação entre Max-Planck-Institut für Limnologie, Abteilung Tropenökologie, Plön, Alemanha, e Instituto Nacional de Pesquisas da Amazônia, Manaus-Amazonas, Brasil

Ecological Studies of the Aquatic Soil Invertebrates in Three Inundation Forests of Central Amazonia

by

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1. Introduction

The first research worker who, from an ecological few point, was able to perceive and describe Amazonian nature as a unity was the swiss anatomist Hans BLUNTSCHLI (1921). Research on the rain-forest ecosystem (FITTKAU & KLINGE 1973) and the productivity of Amazonian water bodies (FITTKAU et al. 1975) were made only in the last few years. The ecosystem approach in Amazonia started with the investigation of the running waters (SIOLI 1968 c, FITTKAU 1971 b), which are one of the most important factors in the overall ecology of the Amazon region (SIOLI 1965 b).

The existence of large inundation forests in Amazonia which, in their extent are unique in the world, most clearly shows the physical effect of the rivers in the landscape (MOREIRA 1970). The várzea, the inundation area of the Amazonas-Solimões and its white water affluents, alone covers an area of 1-2 % of the total hylaea (SIOLI 1956 a). In addition to its physical importance, the inundation forest, together with the phytoplankton of the open water, and the vegetation of the floating meadows (SIOLI 1968 b, JUNK 1970, SCHMIDT 1973), plays an important role in the nutrition of the aquatic systems. This is due largely to falling leaves and fruits etc. During the high water it provides a retreat and source of food for many fish and therefore also for the human inhabitants who rely on fish for their protein source. Furthermore the inundation forest has a braking effect on the river current and thereby directly influences the important sedimentation in the várzea (SIOLI 1957).

There are further reasons why the inundation forest is of special interest to the ecologist. Because of the peculiar and often extreme ecological conditions in this area one can expect a number of interesting ecological adaptations in the flora and fauna. Very few investigations have, until now, been made on this. SIOLI (1954) first drew attention to the many ecological problems in the inundation forest. In recent years, terrestrial soil invertebrates in particular have been studied by BECK (1969, 1971, 1972). Preliminary research on the aquatic bottom fauna resulted in the inundation forest being subdivided on biotic community aspects (IRMLER 1975). The three inundation forests, studied in this project occur in three different water types. The first occurs in the white water type (Ilha de Curari), the second in a mixed water strongly influenced by white water (Lago Janauari), and the third in the lower course of a rain-forest stream (Rio Tarumã Mirim).

The most urgent task among the many new problems in this biotope was to investigate the ecology of the aquatic macroinvertebrates of the bottom fauna. An attempt was made therefore to discover the fundamental ecological relationships and the corresponding adaptations to them.

Acknowledgements

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2. General description of the investigation area

2.1. Geology and climate

Several reports have been published concerning the importance of the geology for the water bodies and general ecological structure of the Amazon region (SIOLI 1968 a, FITTKAU 1971 b, 1974). Therefore only the conditions in the vicinity of Manaus will be briefly described. The várzea, a unique element in middle and lower Amazonia, is the sedimentation area of the alluvium of the Amazon-river and its white water affluents. The rest of the area consists of the strongly weathered deposits of the Pliocene-Pleistocene freshwater sea. In these weathered nutrient-poor soils the rain-forest streams arise, which in the area of Manaus contain black or acid clear water. The water chemistry of the clear water rivers differ, however, depending on the geological make-up of the region (SIOLI 1965 a, 1967).

According to the water chemistry of these river types, the inundation forests differ in their character (SIOLI 1951 b).

The climate in the area of Manaus is described according to the abbreviations of KÖPPEN as "Amwi" (REINKE 1962). *

2.2. Water level fluctuation

In addition to the different water types, the high annual water level fluctuations in the area of Manaus are the most conspicuous phenomenon for an observer of the waters. These fluctuations are therefore of considerable ecological importance. The water level fluctuations become lower towards the lower course of the Amazon-river (GESSNER 1961). At Manaus, the average fluctuation measured over 70 years is 10.10 m. This century the lowest water level during the low water period at Manaus was 14.02 m in 1902; the highest was 21.24 m in 1913 (according the water level measurements in the port of Manaus). The lowest water level during the high water period was 21.77 m in 1926; the highest 29.69 m in 1953. The mean water level at low water amounts to 17.49 m, the mean high water to 27.60 m. In the years 1971/72, during the research, the water level rose higher than the

* No month has a lower mean temperature than 18°C, the most arid month has <60 mm with an annual mean rainfall of 1000-2500 mm and a dry season in summer; the annual temperature fluctuation lies below 5°C.

mean water level. High water in 1971 went up to 29.12 m resp. 28.70 m in 1972, whereas low water even rose to 21.14 m in 1971 (Fig. 1).

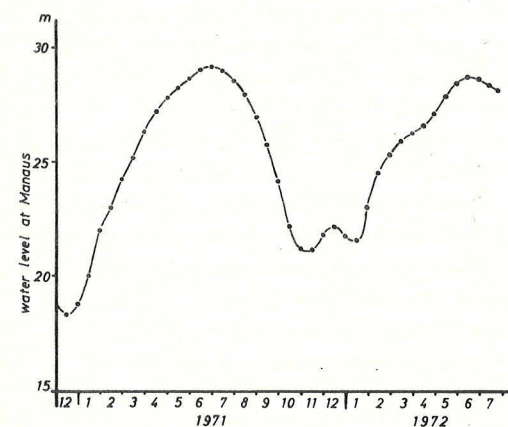


Fig. 1: The water level fluctuations of the Rio Negro at Manaus in 1971/72.

The period of inundation in such extreme water levels differs markedly according to the height of the different forest parts. The higher lying areas are only flooded to a shallow depth and for a short time by high water, whereas the lower lying areas may be flooded even at low water.

2.3. Vegetation and fauna of inundation forests

SIOLI (1954) first detected the biological problems of the vegetation in the inundation forest. Both the oxygen deficit in the deep water, and also the problems associated with photosynthesis during the flooded period demand a particular physiological adaptation by plants to these extreme conditions. Due to the trees annual inundation period can therefore be said to correspond in some respects with the winter of temperate zones. Many plants of the inundation forest develop annual rings (GESSNER 1968). But while in the winter of temperate zones the metabolism decreases, in the inundation forest the high temperatures of the tropics induce a high metabolism. Furthermore the xeromorphic structure of the leaf may be considered as an adaptation to this biotope (GESSNER 1958, 1968).

The differences in water chemistry have a strong influence on the structure of the vegetation (HUECK 1966). In natural conditions the várzea region was covered with forest except for some large areas of lower Amazonia where natural campos were found (BOUILLENNE 1930). Today there are only small areas, not being agriculturally utilized for different reasons, which are covered with natural forest. The forest of the várzea shows a distinct individual character, but is comprised of more species in upper than in lower Amazonia (DUCKE & BLACK 1954).

Characteristic of the lower lying várzea areas and to those subjected to the current, are rapid growing trees like *Alchornea castaneifolia* at Rio Madeira or *Cecropia div. sp.*. In addition, *Inga*, *Acacia*, *Bombax munguba* and the palm tree *Astrocaryum jauary* are also found. The higher lying areas and those not directly subjected to the current are

covered with a high forest consisting of *Ceiba pentandra*, *Olmediophaena maxima*, *Cedrela maxima* etc.. This part of the forest, like the forest on river levees contains elements of the terra firme rain-forest.

The inundation forest, where it is not influenced by white water shows a characteristic vegetation as well. There in particular, trees of the genus *Swartzia*, *Macrolobium*, *Tachigulia*, *Sclerolobium* etc. and the palm tree *Leopoldinia pulchra* (Jará) are found (HUBER 1909). Frequently a shrub formation of *Eugenia div. sp.*, *Symeria paniculata*, *Campsiandra laurifolia* etc. grows in front of the higher forest (TAKEUCHI 1962).

The different conditions found in the big rivers, together with the fluctuations in the water level, have a considerable effect on the fauna just as on the vegetation. Research on the terrestrial soil invertebrates showed that the highest abundance and biomass was in the várzea forest (BECK 1971). In contrast to the situation in the terra firme, a rich macroinvertebrate fauna of soil was found in the inundation forest. Spiders and beetles were particularly abundant (SCHUBART & BECK 1968). A characteristic ecological feature in the inundation forest are movements of many animals in front of the rising water (BECK 1972, 1975) or on the tree trunks which rise above the water, such as shown by the Cicindelidae *Pentacomia egregia* CAUD. An adaptation corresponding with the migration is the orientation mechanism (SCHALLER 1969, IRMLER 1973). Other terrestrial soil invertebrates are able to remain in the forest under water during the high water phase, such as the parthenogenetic females of the Oribatei *Rostrozetes foveolatus* SELNICK (BECK 1969).

A preliminary investigation of aquatic macrobenthos resulted in a division of the inundation forest of Central Amazonia according to the physical and chemical factors and the occurrence of indicator organisms (IRMLER 1975). For instance *Campsurus notatus* NEEDH. & MURPHY is found particularly in várzea forests with an inflow only by white water, *Eupera simoni* JOUSSEAUME in mixed water strongly influenced by white water and the Naididae in the lower courses of rain-forest streams.

3. Methods and terms

3.1. Sampling and analysis

Sampling was carried out at periodic intervals in three sampling areas from May 1971 to August 1972. These areas were: 1. a site with an inflow of white water on Ilha de Curarí, 2. a site in a mixed water area at Lago Janauarí and 3. a site in a black water area at Rio Tarumã Mirim (Fig. 2). In these three forests several sampling stations were chosen differing in altitude and therewith also in inundation duration. There were four stations in the inundation forest on Ilha de Curarí, six at Lago Janauarí, and seven at Rio Tarumã Mirim. Usually every three weeks three samples were taken at each of these seventeen sampling stations. During the phase of rapidly rising and falling water two fortnightly sampling programmes were inserted. The actual sampling was done using a Birge-Ekman bottom sampler of size 15 cm square.

The biomass values refer to the wet weight of the animals. With bottom fauna the dry weight amounts to 20 % of wet weight (WINBERG 1971). When weighing the molluscs, the shell was not removed. In addition to the weight of the shell, wet biomass data of bivalves include water enclosed in the mantle cavity.

pH, temperature, conductivity, dissolved oxygen concentration and transparency were also measured at the sampling stations. Further details on the water analysis methods are given by SCHMIDT (1972 b). At two stations on Ilha de Curarí and at Lago Janauarí particle size of the soil was determined.

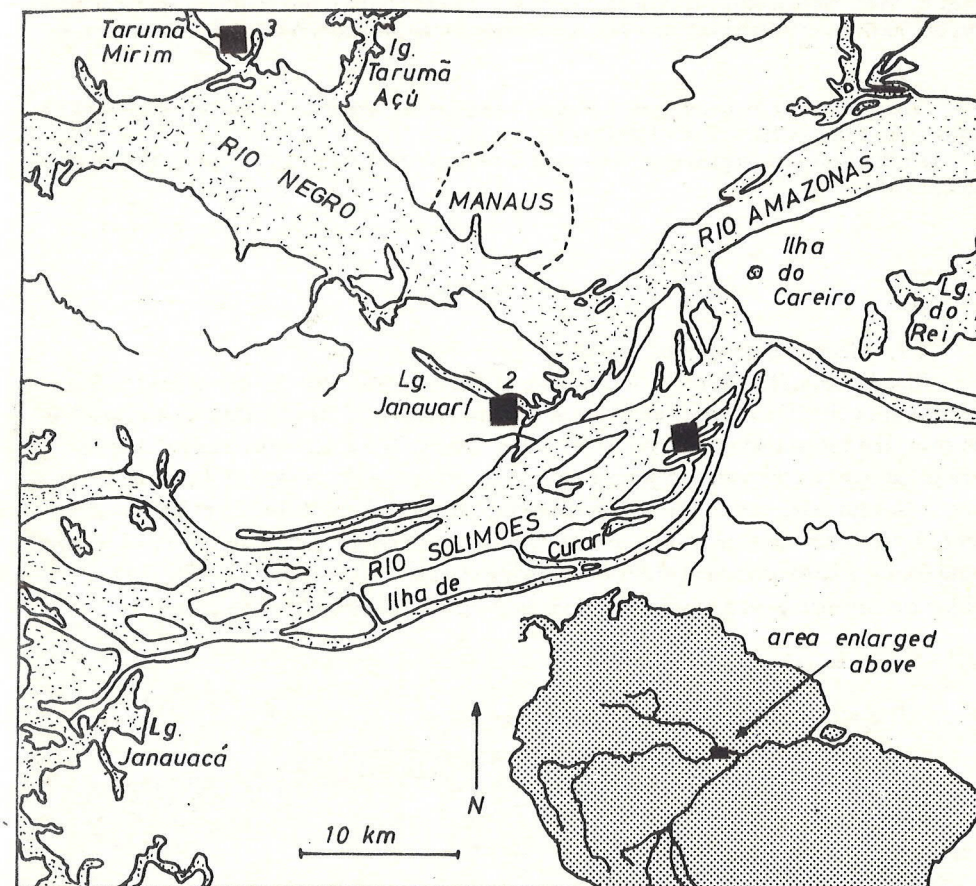


Fig. 2: The three sampling areas 1 - Ilha de Curarí, 2 - Lago Janauarí, 3 - Rio Tarumã Mirim.

At one of the stations lying in the center of the forest three litter samples were taken to obtain the dry weight of the litter at the beginning and at the end of the inundation period.

For the investigations on feeding habits, the intestinal content of 300 animals was studied over the period of one year. Experimental methods are described with the experiments themselves, later in the text.

3.2. Methodological error

Because the areas studied were forest biotopes with a litter layer, leaves and branches interfered with the sampling grab. This has undoubtedly resulted in sampling errors. Only in the data from the inundation forest on Ilha de Curarí where the bottom contains only small amounts of leaf litter was this error greatly reduced. In spite of all efforts in the two other areas, the bottom sampler did not always close completely.

A rough estimation of the methodological error was obtained by a comparison between two different methods of quantitative sampling of *Eupera simoni*. This bivalve lives in the forest during low water. During falling water, comparative sampling was carried out on the shoreline with a bottom sampler in the water and with a quadrat of size 33 cm square on dry land. From this quadrat, litter was col-

lected by hand. The use of this comparative method at two stations resulted in differences between the sampling methods of a factor of four. With smaller animals the methodological error may be greater.

3.3. Terms

Terms pertaining to productivity were used according the definitions of the IBP-program (WINBERG 1971, EDMONDSON & WINBERG 1971).

Further general ecological terms were used in the sense of SCHWERTFEGER (1963, 1968) and BALOGH (1959).

4. Ilha de Curarí

4.1. General description

Ilha de Curarí lies near the south bank of the Amazon river, 15 km upstream from the mouth of the Rio Negro (quadrat 1 in Fig. 2). Because of its situation on an island in the river, the forest receives only a white water inflow. The forest area studied was the only place covered with an acceptable natural forest in a wide vicinity of Manaus. Its presence at this side was due to the strong river current which kept it free from human settlement. Thus, the bank here had developed as a Barranco (steep bank), and in 1972, during rising water, a large section in front of sampling station 3 was washed off (Fig. 3) resulting unfortunately in a modification in the benthos community. There were 4

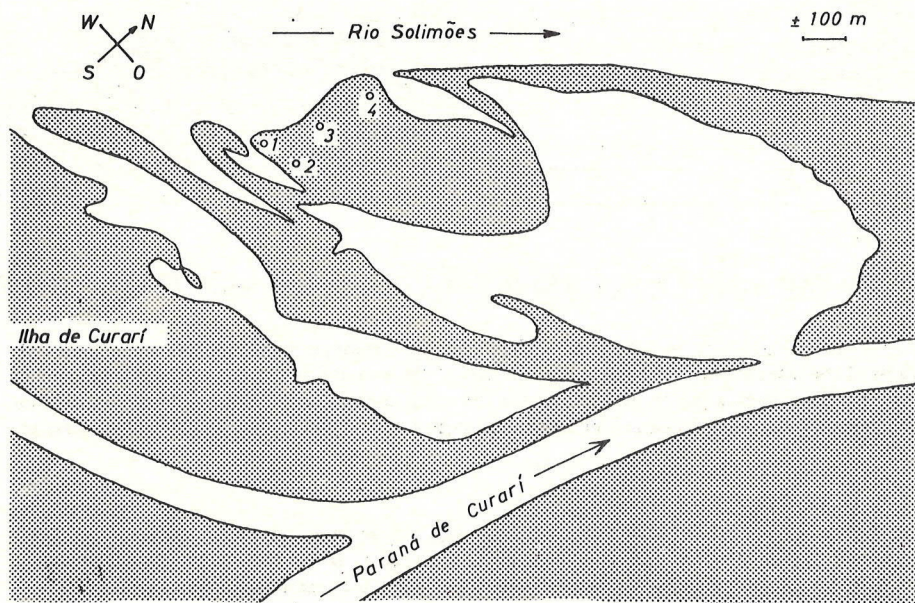


Fig. 3: The sampling area on Ilha de Curarí, showing the four sampling stations.

sampling stations in the studied forest. The highest station lay nearest to the river. The deepest station (No.4) near the lake had a maximum water level of 5.30 m in 1971. This

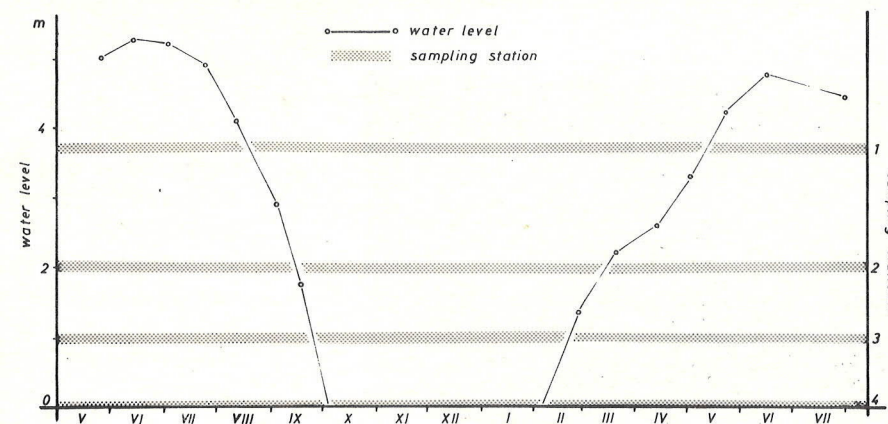


Fig.4: The four sampling stations on Ilha de Curarí according to the water level fluctuation and the inundation period.

station was dry from the middle of October to the beginning of February. The water level and the inundation period of each sampling station may be obtained from Fig. 4.

The following plants could be identified from this area: *Bombax munguba* MART., *Gustavia augusta* L., *Quina rhytidopus* TUL., *Vitex cymosa* BERT., *Cecropia*, *Luffa operculata* COQU., *Homalium pedicellatum* SPRUCE, *Byrsonima*, *Simaba*, *Buchenavia grandis* DUCKE, *Astrocaryum jauary* MART.

4.2. Environmental factors

4.2.1. The substratum

The deposit of the sediment load of the Amazon river is of decisive importance for the fauna. At the narrows of Obidos, 0.1966 g/l suspended solids were determined at the surface (KATZER 1903). SCHMIDT (1972 b) estimated values between 37 and 165 mg/l in Central-Amaozonia upstream from the mouth of the Rio Madeira which is rich in suspended solids. The great sediment load of the Amazon is also expressed by the low transparency, fluctuating only between 0,3 m and 0,45 m. The suspended solid content of the river varies considerably within one year, however. The maximum yield lies in December (SCHMIDT 1972 b). Taking into account annual fluctuations and the variations between several years, differences of 500% may occur (SIOLI 1957). After the water flows into the várzea, a more intensive sedimentation sets in and the suspended matter consists more and more of organic particles (SIOLI 1957). The inorganic components consist largely of quartz, feldspar, clay minerals and other small particles (GIBBS 1967). On Ilha de Curarí particle size composition of the soil at sampling station 1 and 4 was determined. At both sampling stations particle sizes between 63-20 μ m diameter predominate. At sampling station 4 the smaller particles of 20-2 μ m diameter were more frequent than at station 1 which

may be explained by its greater distance from the river. The sediment deposition was estimated by a soil profile after the site dried out. The upper layer contained leaves and other coarse organic matter while the lower layer was relatively homogeneous (Fig. 5).



Fig. 5: Soil profile at sampling station 4 on Ilha de Curari.
a) upper layer containing coarse organic matter
b) lower homogeneous layer

The upper layer at station 4 was ± 17 cm thick and at station 1 ± 8 cm thick. Whether the upper layer deposited during the high water phase or developed by moistening of the original clay, cannot be decided. The leaves within the clay appear to indicate a development during one particular high water phase, however. In this case the mean monthly sedimentation amounts to 2.7 cm at station 1 and 2.1 cm at station 4.

Because during high water a thick sediment layer is deposited, no litter layer occurs at the surface when the dry phase begins (Fig. 5). Up to the beginning of the new high water phase, 3.6 t/ha average dry weight of the litter covers the ground. This litter, present at the beginning of the high water phase but becoming covered more or less rapidly during the inundation period, is of great importance for the development of the benthos community (see chapter 4.3.).

4.2.2. Conductivity

Although by Amazonian standards the white water is chemically "rich", it clearly shows a poverty of dissolved salts. In addition, the buffering capacity, indicated by low alkalinity, Ca^{2+} - and Mg^{2+} - values, is not significant. In particular the low values of NO_2^- , NO_3^- , and PO_4^{3-} are remarkable (SCHMIDT 1972 b). The sediments of the várzea seem to be important as buffering substances for the phosphate concentration (GESSNER 1960 b).

The conductivity of the water in the forest on Ilha de Curari fluctuated in the year of investigation between $27.3\text{--}83.9 \mu\text{S}_{20}/\text{cm}$ (Fig. 6). The highest values could be measured at the beginning and at the end of the inundation period. The conductivity must be seen in close relationship with that of the Amazon because of the immediate proximity of the river. Instead of the regularity of conductivity changes, with a maximum conductivity in December as found by SCHMIDT (1972 b), a more undulating pattern of conductivity was observed which may be explained by the influences of different affluents. In general the conductivity of the water in the inundation forest is lower than that of the Amazon river.

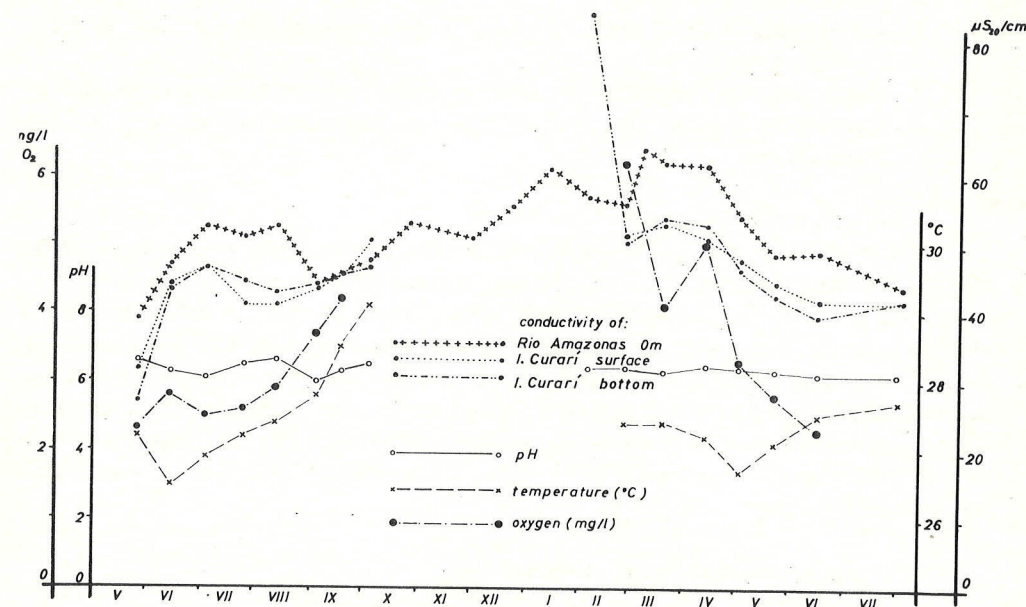


Fig. 6: Conductivity of surface and bottom water at station 4 on Ilha de Curari compared with that of the Amazon during 1971/72, oxygen, pH, and temperature of the bottom water of station 4 on Ilha de Curari.

Due to leaching of the electrolytes, which are produced during the dry phase, high conductivity values occur at the shoreline during rising water. (Uferfaktor of BRAUN 1952).

4.2.3. Oxygen

The pattern of conductivity changes is similar to that of changes in oxygen concentration. During rising water and falling water high oxygen concentrations could be found, whereas during high water relatively low values were obtained (Fig. 6). In the middle of the river, values between 4 and 5 mg/l O_2 during high water were determined. The low oxygen concentration of 2-3 mg/l O_2 in the inundation forest may be explained by the abundant supply of organic matter from the forest, which apparently causes an oxygen consumption of 50 % during its decomposition. The turbidity of the inflowing water prevents an oxygen stratification between the surface and the deep water. The oxygen concentrations in all parts of the studied forest were nearly the same.

The O_2 -production by phytoplankton may be neglected during high water, because only a small phytoplankton abundance exists in the river (SCHMIDT 1970). It is only during the falling water phase when lentic areas are cut off from the river, that the oxygen supply may rise due to the increasing phytoplankton production.

The oxygen concentration and conductivity curve of the inundation forest on Ilha de Curari can be subdivided in three phases:

1. a lentic phase with relatively high oxygen concentrations and conductivity during rising water;
2. a lotic phase with relatively low conductivity and oxygen concentrations and
3. a second lentic phase during falling water with increasing conductivity and oxygen concentration.

4.2.4. pH and temperature

The pH of white waters shows only small fluctuations from near neutrality (SCHMIDT 1972 b). A relation between water level fluctuations and pH or temperature could not be found (Fig. 6). Both the pH and the temperature on Ilha de Curarí fluctuate in the same way as the Amazon river water in front of the island, between 6.0 and 6.6, and 26.5°C and 29.1°C respectively. The temperature increase at the end of the high water period may be due to the higher insolation during the dry season. Neither the temperature values nor the oxygen concentrations varied between the surface and the deep water as in the strong current of the Amazon, with values up to 1.3 m/sec (GESSNER 1961), a temperature stratification cannot develop.

4.3. The macroinvertebrates of the benthos

4.3.1. Seasonal periodicity in the community composition

The fauna of the inundation forest is made up largely of Ephemeroptera, Chironomidae and Bivalvia. The remaining organisms make up only 7.2 % of the total and can be considered negligible. In terms of abundance, Oligochaeta and Ostracoda are also numerous. The most important species of the first mentioned groups are *Campsurus notatus* NEEDH. & MURPHY (Ephemeroptera, Polymitarcidae), *Brasilocaenis irmieri* PUTHZ (Ephemeroptera Caenidae), *Pisidium sterkianum* PILSBRY (Bivalvia, Sphaeriidae) and *Chironomus gigas* REISS (Diptera, Chironomidae) (Table 1).

The composition of the community varies within one year, showing a characteristic periodicity which may depend on the water level fluctuations and the changing environmental conditions connected therewith (Fig. 7).

The characteristic species at rising water are : *aff. Aphylla*, *Laevapex aguadae*, *Brasilocaenis irmieri*, Culicidae, *Chironomus latistylus* and *Chir. sp. AR 4*; at high water : *Eupera simoni*, *Eupera bahiensis*, *Laevapex aguadae*, *Brasilocaenis irmieri*, *Campsurus notatus*; at falling water : *Campsurus notatus*, *Chironomus gigas* and Culicidae.

This annual periodicity of several species suggests changing environmental conditions during the inundation period. It is worth noting, that of the eleven differentiated taxa, only very few occur during the falling water phase - although they are found in high abundances (Fig. 8). This, according to the second ecological principle of THIENEMANN (1918), indicates living conditions becoming more extreme.

4.3.2. The vertical stratification of the fauna

Before going further into the reasons for the seasonal periodicity, it is necessary to describe the vertical stratification of the fauna. Only those species showing a typical stratification are described. *Opisthocysta flagellum* LEIDY (Oligochaeta, Opisthocystidae) is apparently tolerant to a wide range of conditions, as shown by its vertical stratification. Although the number of individuals of this species varies both within one season and at each station, it nevertheless occurs in fairly high abundances (Fig. 9).

Table 1: The differentiated taxa of the inundation forest on Ilha de Curarí (A - % of annual mean abundance, B - % of annual mean biomass).

taxonomic group	% A	% B	taxonomic group	% A	% B
NEMATHELMINTHES			Insecta		
Nematoda			DIPTERA	45.4	24.6
			Chironomidae		
PLATHELMINTHES			<i>Chironomus gigas</i> REISS		
Turbellaria	2.3	0.4	<i>Chironomus latistylus</i> REISS		
			<i>Chironomus sp. AR 4</i>		
MOLLUSCA			<i>Stenochironomus</i>		
Bivalvia	4.2	14.5	further Chironomini species		
<i>Pisidium sterkianum</i> PILSBRY			Tanytarsini		
<i>Eupera simoni</i> JOUSSEAUME			Tanypodinae		
<i>Eupera bahiensis</i> SPIX			Orthocladinae		
Gastropoda	2.9	1.1	Culicidae		
<i>Hebetancylus moricandi</i> D'ORB.			Ceratopogonidae		
<i>Laevapex aguadae</i> GOODRICH & v. d. SCHALIE			Chaoboridae		
			Brachycera larvae		
<i>Ampullarius</i>			TRICHOPTERA	1.4	0.6
Planorbidae			ODONATA	0.5	1.4
			Zygoptera		
ANNELIDA			<i>aff. Aphylla</i>		
Oligochaeta	10.3	1.4	further Anisoptera species		
<i>Opisthocysta flagellum</i> LEIDY			COLEOPTERA		
Hirudinea	0.2	0.3	Dytiscidae		
			EPHEMEROPTERA	21.3	53.7
ARTHROPODA			<i>Campsurus notatus</i> NEEDH. & MURPHY		
Acari			<i>Brasilocaenis irmieri</i> PUTHZ		
Crustacea			Ephemerellidae		
OSTRACODA	5.4	0.2			

In contrast, the following groups show a specific periodicity and stratification. First *Brasilocaenis irmieri* and *Laevapex aguadae* progress through two clear phases, one during the beginning of inundation at station 4 and one during high water at station 2 (Fig. 9). It may be suggested by this stratification, that with rising water the living conditions for the animals at station 4 become unfavourable. The population of the station 4 dies out, while a new population develops at station 2. *Eupera* is more specific in its habitat requirements. These bivalves only occur during high water at station 2. *Aff. Aphylla*, which could be found during rising water at station 4, has an equally short existence. In contrast, *Pisidium sterkianum* avoids those habitats which are favourable to *Eupera*. *Pisidium sterkianum* prefers the deeper stations. A similar stratification is shown by *Campsurus notatus* which clearly prefers station 3 and 4. Only single individuals of this mayfly occur during high water in the shallow flooded area (Fig. 9).

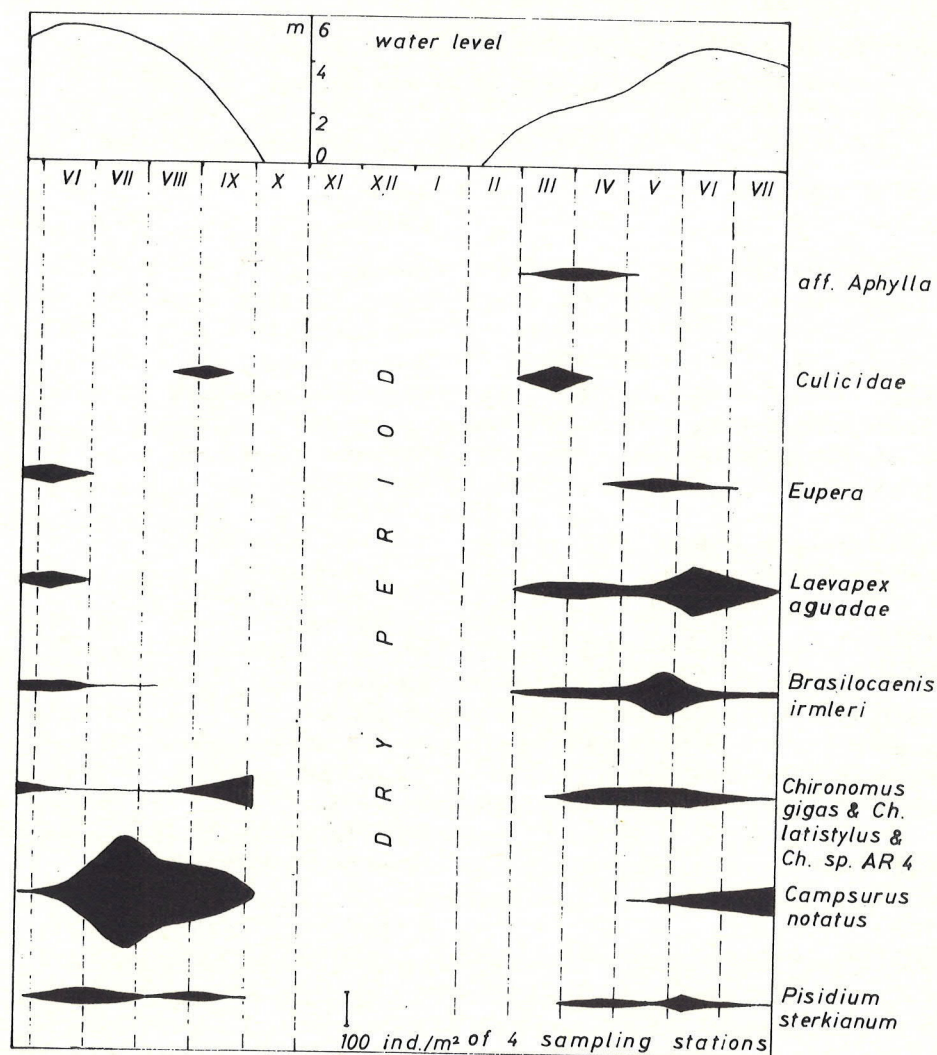


Fig. 7 : The annual distribution of different species compared with the water level fluctuations on Ilha de Curari.

Thus, the stratification of the fauna shows a differentiated and dynamic structure. Comparing the seasonal periodicity with the vertical stratification, the organisms could be divided into those with a relatively wide range in periodicity and stratification, and those which obviously demand specific environmental conditions. Those organisms which can avoid the deteriorating environmental conditions like *Brasilocaenis irmleri* and *Laevapex aguadae* occur for longer periods, whereas those organisms which apparently don't have this capacity like *aff. Aphylla* and *Eupera* are only found for a short period

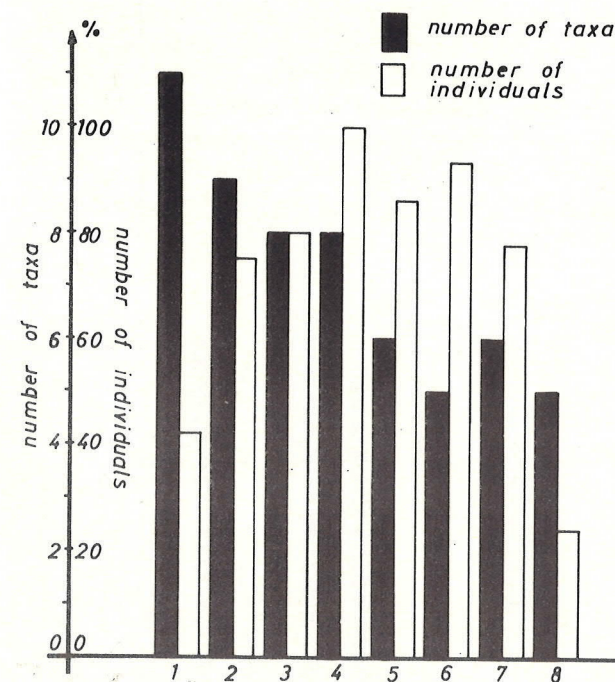


Fig. 8: The number of differentiated taxa compared with that of individuals occurring in eight successive series of samples from high water 1971 till low water on Ilha de Curari.

each year. The habitats evacuated by one set of species will be occupied by another. The annual periodicity and the stratification appear to be related, as it is reflected by the seasonal changing communities (german term "Aspekte"):

1. The community of rising water at station 4 (low flooded area up to ± 2.5 m water level): *Brasilocaenis irmleri*, *Laevapex aguadae*, *aff. Aphylla*, *Opisthocysta flagellum*, *Chironomus latistylus*.
2. The community of high water at station 2 (low flooded area up to 2-3 m water level): *Brasilocaenis irmleri*, *Laevapex aguadae*, *Eupera simoni*, *Eupera bahiensis*, *Opisthocysta flagellum*, *Chironomus latistylus*.
3. The community of high water - falling water at station 4 (high - low flooded area): *Campsurus notatus*, *Chironomus gigas*, *Pisidium sterkianum*.

4.3.3. The most important factors for the periodicity and the stratification of the fauna.

In examining the factors responsible for regulating the community structure, those which do not show a conspicuous annual fluctuation such as pH and temperature can be excluded. Changes in oxygen concentrations and conductivity may be important for the

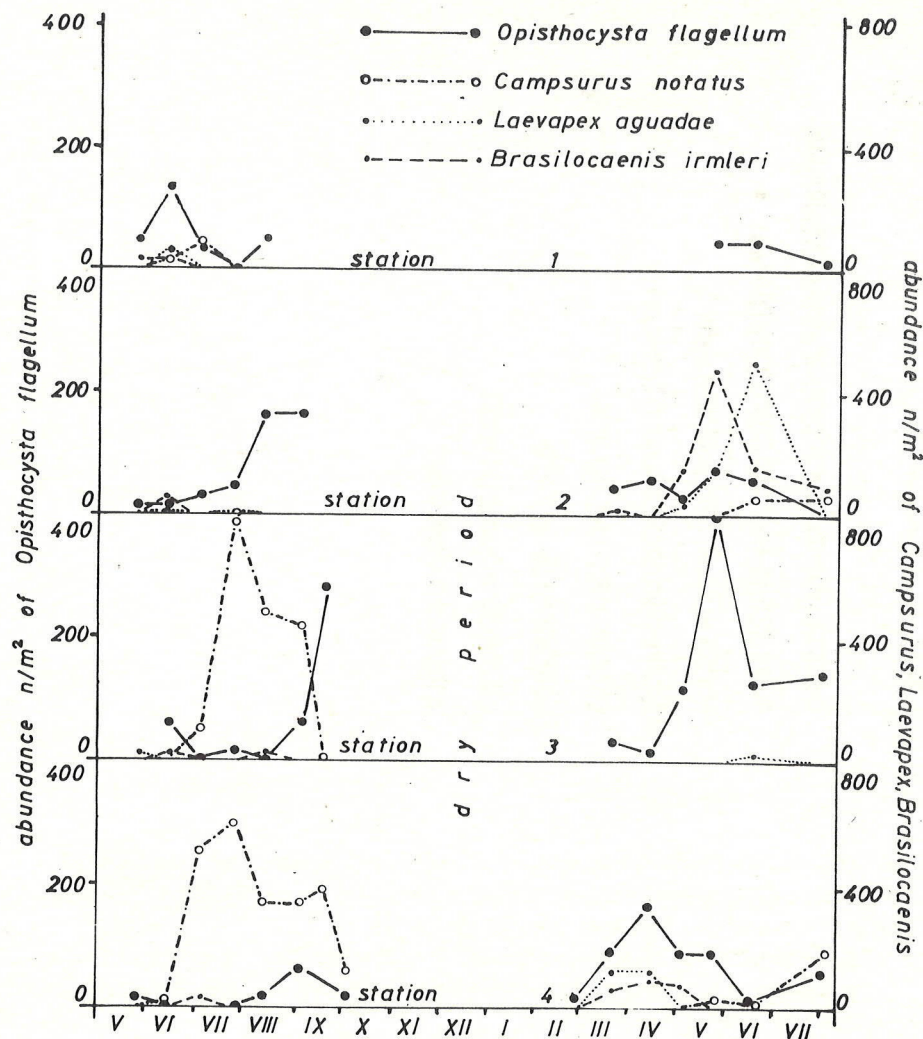


Fig. 9 : Distribution of *Opisthocysta flagellum* LEIDY, *Campsurus notatus* NEEDH. & MURPHY, *Laevapex aguadæ* GOODRICH & v. d. SCHALIE, and *Brasilocaenis irmleri* PUTHZ on Ilha de Curari.

seasonal periodicity of the fauna. Both factors cannot, however, control the stratification of the fauna because no differences of oxygen concentration and conductivity could be obtained within the different parts of the forest. On the other hand, the role of sedimentation, and the corresponding change of the substratum seem to be important. Leaf litter existing at rising water is covered by sediment more and more with continuing inundation. This happens first at the place with the longest inundation time (station 4). Organisms

which depend on a leaf litter have to migrate or must complete their development before the litter is covered too deeply.

The result of two experiments with organisms which depend on a leaf litter seem to support this theory. The effects of sediment on the development of the mayfly *Brasilocaenis irmleri*, were investigated in three different cultures. Three samples were taken. One of them was sieved to remove the mud, another was only partly sieved, and for the last the original substratum was used. The samples came into the laboratory at 28-6-72 and contained at that time no mayfly larvae. During the experiment the hatched imagoes were counted. The result shows clearly that the individuals develop better on leaf litter than in the mud (Fig. 10). Furthermore, in this experiment the individuals must have

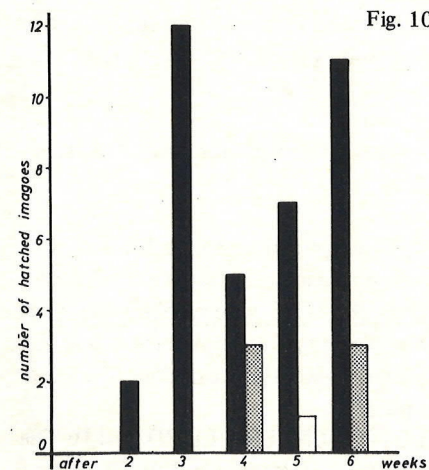
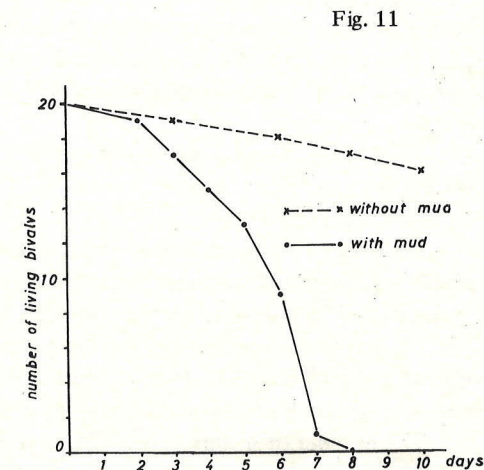


Fig. 10 : Number of hatched imagoes of *Brasilocaenis irmleri* PUTHZ in three different cultures (black - sieved sample, dotted - partly sieved sample, white-original substratum).

Fig. 11 : Stress test with *Eupera simoni* JOUSSEAUME to being covered with mud.



been in the samples as eggs. The rapid development from the egg to the imago within 2-3 weeks shows that the species is extremely well adapted to overcome the problems of changing environmental conditions. It is difficult to determine whether the eggs were initially in the mud or in the added water. It is suspected, however, that the eggs are transported by the water, and develop where they find favourable environmental conditions.

In a second experiment, the tolerance of *Eupera simoni* to being covered with sediment was investigated, by placing the bivalves in a gaze bag and covering them with mud (Fig. 11). This experiment also shows the limiting effect of the mud cover. After one week hardly a single individual of the original 20 specimens was alive. The importance of the leaf litter for the ecology of *Eupera simoni* will be described further in chapter 5.3.3..

The first community of station 4 and that of station 2 apparently consists of species which depend on a firm substrate. As the deposition of sediments continues that community will die out. Some species with a rapid development succeed in settling on other more favourable places. The species of the second community at station 4 live in the mud. *Campsurus notatus* is apparently adapted to a borrowing activity, building canals in the substratum (SATTler 1967). The reason why the population of these animals does not increase with continuing sediment deposition at station 1 and 2 can only be suggested. On the one hand, the inundation period may be too short for their lengthy development time, and on the other hand, the deposited suspended solids may contain a large amount of coarse particles (see chapter 4.2.1.). The fact that a great sediment load acts as a limiting factor for filter feeders has already been shown in the faunal community of the floating meadows (JUNK 1973). The absence of *Campsurus notatus* at station 3 in 1972 can be accounted for by the nearness of the river. In front of station 3 a 30 m wide patch of the forest was eroded off, as mentioned earlier, thus bringing the river closer to this station.

4.3.4. Population dynamics of *Campsurus notatus*, *Chironomus gigas*, *Pisidium sterkianum*, and *Eupera simoni*

Campsurus notatus

An attempt was made to study productivity, development, age distribution and possible migrations of the most important species. A population consisting of different age classes can be described by the equation $N_{i+1} = N_i + B - D + I - E$, where: N_i = total number of individuals in the population, B = birth rate, D = mortality, I = immigration, and E = emigration (WILLIAMSON 1972). Because the studied population consisted of insect larvae no increase by birth within one size class is possible.

The number of instars in mayflies is very high (WESENBERG-LUND 1943). The larvae of the population of *Campsurus notatus* in the studied inundation forest show at least 13 instars which can be obtained by measurement of the head length (Fig. 12).

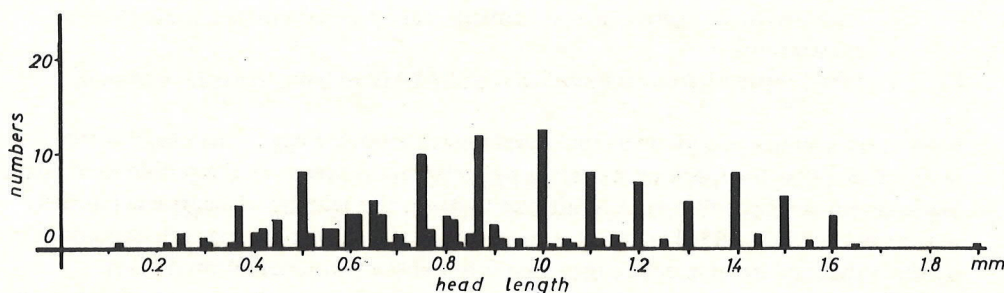


Fig. 12 : Number of larvae of *Campsurus notatus* NEEDH. & MURPHY with different head lengths. All larvae of the whole investigation period were measured.

Fig. 12 shows, however, that the young larvae were underrepresented. With proceeding development, mortality brings about a decrease in the number of larvae. This difference between the theoretically required and actually observed number of individuals of the

young larvae may be due to a sampling error such as the mesh factor (JONASSON 1958). Another reason for this discrepancy may be the immigration of the small larvae. By estimating the hypothetical number of young larvae (ALLEN 1951), a mortality of at least 22 % must be taken into account (estimated average mortality). The number of young larvae obtained hypothetically by the ALLEN-curve amounts to $\pm 1200 \text{ n/m}^2$ for both generations.

Campsurus notatus probably migrates as can be shown by Fig. 13. The instars were

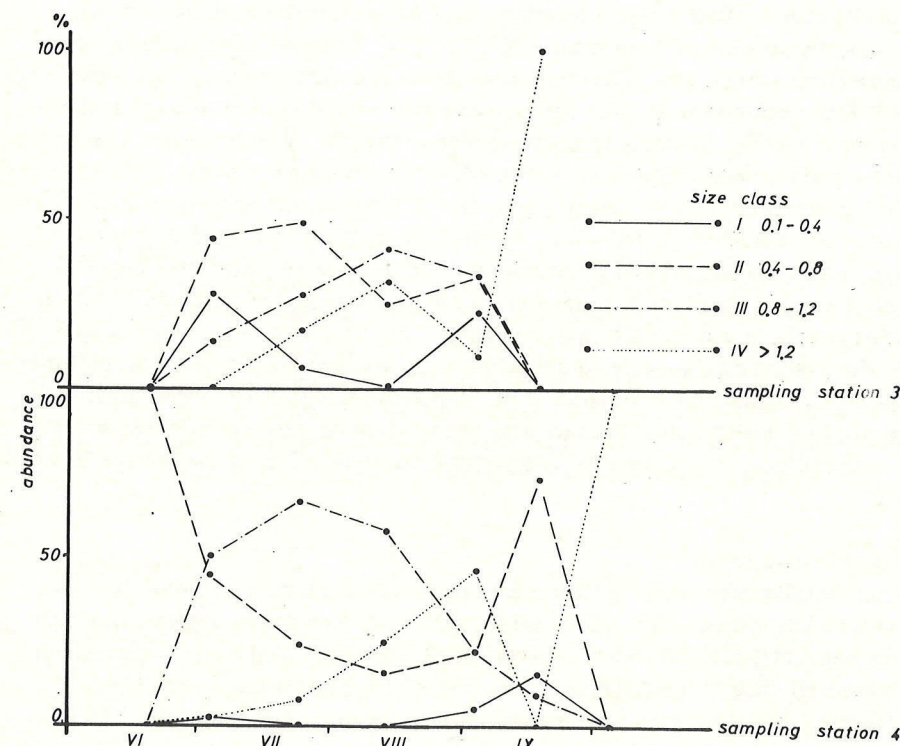


Fig. 13 : Distribution of the four size classes of larvae of *Campsurus notatus* NEEDH. & MURPHY at the stations 3 and 4 on Ilha de Cururí.

divided into four size classes. As was expected, young larvae predominate in the early stages. Only in August and at the beginning of September did large larvae appear. After hatching in September a new increase of young larvae occurred. As the water level fell further, however, the young larvae could not be found at the sampling areas as may be expected if one considers larval development. In contrast, a concentration of large larvae appeared at station 3 and 4. This phenomenon can only be explained by an emigration of young larvae and only a slow migration of the larger larvae in breeding condition with the falling water. No larvae of *Campsurus* could be found on dry land as was the case with

Chironomus gigas. Fig. 13 also shows that larval development lasts 2 1/2 - 3 months.

To show the growth curve of *Campsurus notatus*, weights and head lengths were compared on individual animals. A larvae grows up to 22 mg in weight. The population increase cannot be calculated exactly because of the role of immigration and emigration in the population-dynamics of *Campsurus notatus*.

Chironomus gigas

The population-dynamics of this species could not be investigated as thoroughly as the preceding species. Taxonomic research on the *Chironomus* larvae of this area has resulted in the separation of three species (REISS 1974). Till now, only the larvae of the three species *Chironomus gigas*, *Chironomus latistylus* and *Chironomus* sp. AR 4 could be separated. The maximum abundance shown by *Chironomus* at the end of the inundation period at station 4 (Fig. 7) was in fact attributable to the first of these species. During the rising water period, *Chironomus latistylus* and *Chironomus* sp. AR 4 occur.

The age distribution of the larval population of *Chironomus gigas* was studied. The young larvae are underrepresented with respect to the length-frequency distribution. At the end of the inundation period an increase in the abundance of large larvae appears. Two comparative samples taken in the water and on dry land may give an estimate of the migration ratio of the larvae. In both cases 356 n/m² were obtained. In the water only 62 % larvae of the largest size class were found, whereas on dry land 86 % occur. This indicates, that large larvae are not able to emigrate with falling water, whereas younger larvae have this capacity to a small extent. No exact data can be given concerning the development time. It seems to be 1 1/2 - 2 months. The younger larvae of ± 2 mg grow to large larvae of 15-16 mg.

Pisidium sterkianum

An interesting adaptation to the ecological conditions of the inundation forest was found with *Pisidium sterkianum*. This bivalve produces two generations within one year: one at the beginning of the inundation period up to high water, and a second from high water to the beginning of the dry period (Fig. 14). The average weight of the bivalve increases from 0.1-0.2 mg of young bivalves up to ± 30 mg for gravid animals. Gravid individuals were found in July and September/October. With falling water the gravid bivalves remain on dry land. In the last samples, bivalves could be found both on dry land and in the water. Once, during the dry period, young animals were found living between the valves of the dead adult. It therefore appears, that the young bivalves are covered by the valves of the adult during dry period and then leave this shelter with rising water.

Of the other species of the genus *Pisidium* of the South-American tropics, only the population-dynamics of *Pisidium forense* MEIER-BROOK has been described thoroughly (MEIER-BROOK 1970). Fundamental differences occur between the two species. *Pisidium forense* has two breeding phases with a continuous development cycle. Both gravid and young bivalves could be found continuously side by side. In contrast, *Pisidium sterkianum* has an annual periodicity induced by the water level fluctuations. It is not yet clear whether the adults of the first generation breed a second time. Although large mature individuals could not be found between the two different generations, this may have been

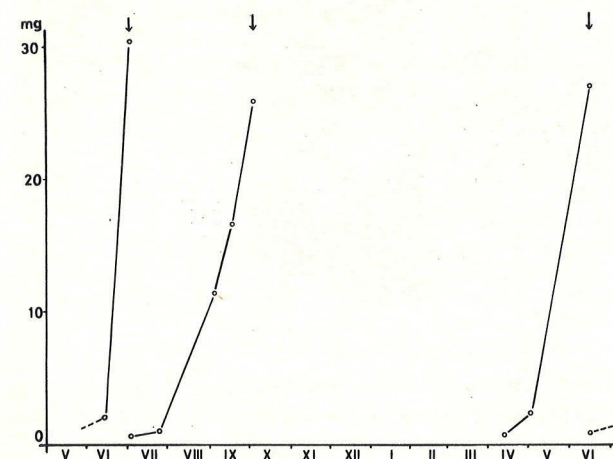


Fig. 14: Mean weight of an individual of *Pisidium sterkianum* PILSBRY during 1971/72 on Ilha de Curarí. Arrows indicate the time, when gravid individuals were found. The broken lines indicate the further hypothetical course of curves.

due to their low abundance.

No exact data can be given on the mortality of this bivalve, because the abundance was too low although the following figures may be indicative. The number of young bivalves per adult amounted to 9-12. From the average abundance of the young bivalves in July (± 290 n/m²), 15 n/m² gravid bivalves remained at beginning of the dry period. Thus, mortality could have accounted for 95 % of the animals. In the last generation ± 170 young bivalves/m² were produced. Only ± 60 n/m² survived the dry period. That means, that ± 65 % of the young bivalves died during the dry period. The survivors a further 45 % died before reaching the adult stage.

Eupera simoni

The abundance of *Eupera simoni* in the inundation forest on Ilha de Curarí is very low. Therefore, in this chapter only its development in this region may be described. Further details of the population-dynamics are found in chapter 5.3.4.. On Ilha de Curarí gravid bivalves occurred in May-June. The number of young bivalves in the gill bags amounted to 15-29. At this time the population consisted of 80-90 % of young bivalves. It is probable that young bivalves immigrated into this biotope during the high water period, because the animals died out within the benthos community during high water.

4.3.5. Feeding habits

To detect the trophic level an animal occupies within an ecosystem, it is necessary to obtain data on the quality and quantity of its diet. No work was done on the quantity of the food ingested, but qualitative aspects were studied by investigations on the intestinal contents. According to their life form, animals differ in their mode of feeding.

Campsurus notatus, the most important species in the inundation forest on Ilha de Curarí, is a borrowing animal. It probably filters food particles from the water with the aid of filtering hairs on the forelegs (SATTler 1967). The intestinal content consists of clay material and leaf fragments in particular. The species of the genus *Chironomus* have similar intestinal contents, although coarse leaf fragments are more frequent (Fig. 15).

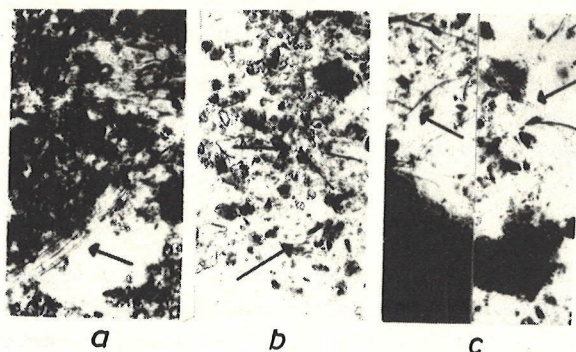


Fig. 15: Leaf fragments in the intestinal content of *Chironomus gigas* REISS (a); fragments of fungi in the intestinal content of *Brasilocaenis irmieri* PUTHZ (b); setae of Naïdidae in the intestinal content of *Euryrhynchus burchelli* CALMAN.

The other species of the Chironomidae except the Tanypodinae, also feed on leaf fragments. The bivalves *Pisidium sterkianum* and *Eupera* are also detritivores. Whether these detritus-feeding animals feed also on microorganisms cannot be decided here.

Only few reports have been published on filtering rates of freshwater bivalves. In the temperate zones 10-20 ml/1 g weight per hour are known for *Pisidium*. Temperature, however, influences the filtering rate (HINZ & SCHEIL 1972).

Predators like Anisoptera and Tanypodinae mainly feed on Ostracoda and Chironomidae. Table 2 shows the diet of different organism groups. Obviously organisms of the detritus food chain predominate. Fungi and phytoplankton were not often found in the intestinal contents. The low amounts of phytoplankton as food source for the benthos community can be explained by the low primary production in white waters (SCHMIDT 1970). About 70 % of the benthos community according to annual biomass obtain their food from the litter (73,6 % feed on coarse detritus particles or leaf fragments, 13,2 % feed on small detritus particles, 2,8 % feed on detritus and fungi and 6,8 % are predators). Thus, the benthos community may be important for the breakdown of the leaf litter. Whether the detritivores act as primary or secondary decomposers is open to question. They can probably fulfil both functions as has been shown for chironomid larvae (DÖLLING 1962).

A relationship between feeding habits and the available prey could be detected for the Tanypodinae. During the maximum abundance of the Ostracoda they feed exclusively on Ostracoda. But with decreasing abundance of the Ostracoda and increasing abundance of the Chironomidae their diet consisted more and more of Chironomidae. Finally only Chironomidae were found in the intestinal contents (Fig. 16).

4.3.6. Productivity

Due to the migrations of the fauna it is extraordinarily difficult to describe the productivity of the total forest area. The following account of productivity, therefore, applies only to the four investigated sampling stations.

Table 2: The composition of the intestinal content of different taxa on Ilha de Curari

Detritivores	
<i>Campsurus notatus</i>	: mainly - coarse detritus and leaf fragments less - fungi and algae
Chironomini	: mainly - coarse detritus and leaf fragments less fungi and algae
Sphaeriidae	: small detritus particles, sometimes fungi
Caenidae	: detritus, sometimes fungi
Ancylidae	: detritus, sometimes fungi
Opisthocystidae	: detritus, sometimes fungi and algae
Predators	
Tanypodinae	: Opisthocystidae, Tanypodinae, Chironomini Ostracoda
Anisoptera	: Opisthocystidae, Chironomini
Ceratopogonidae	: probably haemolymph of chironomids

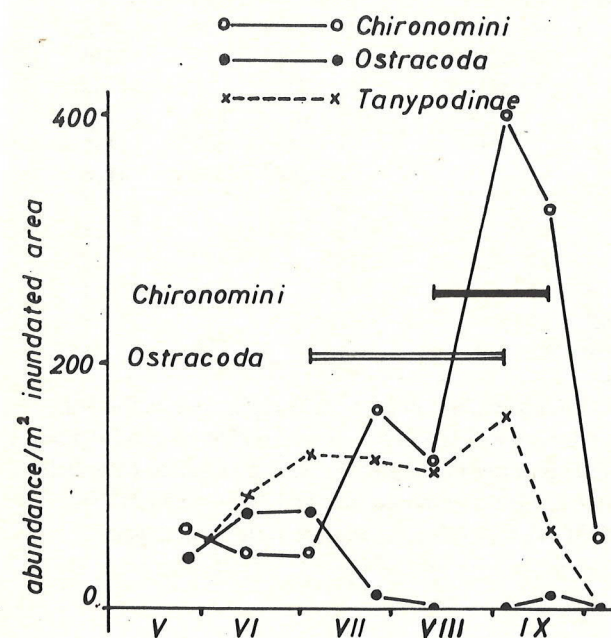


Fig. 16: Predator (Tanypodinae) - prey (Ostracoda, Chironomini) - relationship. The horizontal columns indicate the time in which Ostracoda and Chironomini are fed by the Tanypodinae.

The maximum biomass values amounting to 4.0 and 3.4 g/m² were obtained in the longest flooded area of sampling stations 3 and 4 respectively. The lowest maximum value of biomass 0.3 g/m² was found at station 1. The average biomass values for each sampling station were: 1=0.2 g/m², 2=0.4 g/m², 3=1.1 g/m², 4=1.8 g/m² for stations 1, 2, 3 and 4 respectively (Fig. 17). The different duration of inundation influences the productivity of the different parts of the forest, and must therefore be considered. If the annual biomass of sampling station 4 amounts to 100 %, the following biomass ratios of the different sampling stations can be calculated: 1=4.9 %, 2=16.4 %, 3=57.7 %. *Campsurus notatus* accounts for the largest part of the biomass. In August the biomass of the mayfly species at stations 3 and 4 was 3.5 g/m² and 2.2 g/m² respectively. Further important species are the bivalves *Eupera simoni* and *Pisidium sterkianum*. The highest biomass value of *Eupera simoni* lies at sampling station 2 with 1.2 g/m². That of *Pisidium sterkianum* occurs at station 4 with 1.7 g/m². An important group which could not be broken down further taxonomically, are the chironomids. At the end of the inundation period their biomass amounts to 4 g/m² at station 4 which corresponds with the occurrence of *Chironomus gigas* (see chapter 4.3.4.). The other biomass values of the chironomids lie well below that, around 0.2 g/m² (Table 3).

Table 3: Biomass in mg/m² of *Campsurus notatus* (a), *Pisidium sterkianum* (b), *Eupera simoni* (c) and Chironomini (d) in the 4 sampling stations on Ilha de Curarí.

date	sampling station 1				sampling station 2				sampling station 3				sampling station 4			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
25. 5.71	-	-	-	44	-	-	-	1204	28	-	-	133	29	-	-	-
14. 6.71	76	-	-	16	37	78	400	32	-	-	661	40	7	32	-	14
3. 7.71	176	-	-	-	-	-	-	34	249	32	-	105	1099	1124	-	9
24. 7.71	-	-	-	35	80	3	-	20	3195	7	-	222	2514	29	-	210
13. 8.71	-	-	-	50	-	-	-	9	3511	12	-	84	2247	-	-	62
3. 9.71									1784	-	-	170	2153	848	-	252
17. 9.71									218	7	-	4	467	491	-	1155
4.10.71	DRY PERIOD												2647	332	-	4116
26. 2.72									-	-	-	3	-	-	-	4
20. 3.72					-	-	-	-	-	-	-	13	-	-	-	71
11. 4.72					-	-	-	230	-	12	-	28	-	29	-	53
2. 5.72	-	-	-	-	-	-	-	6	138	-	6	7	-	103	-	14
23. 5.72	-	3	-	16	-	-	-	287	34	-	-	13	-	-	-	4
12. 6.72	-	-	-	1	7	7	90	246	-	-	-	14	3	1780	-	74

The calculation of the production, difficult enough in lakes, is complicated in the inundation forest by the high dynamic periodicity of the fauna. A calculation of production was attempted, however, using the data acquired in chapter 4.2.3.. An estimate was made of the production of *Campsurus notatus*, *Pisidium sterkianum* and *Eupera simoni*. In line with the method of NESS & DUGDALE (1959), the average weight of a cohort

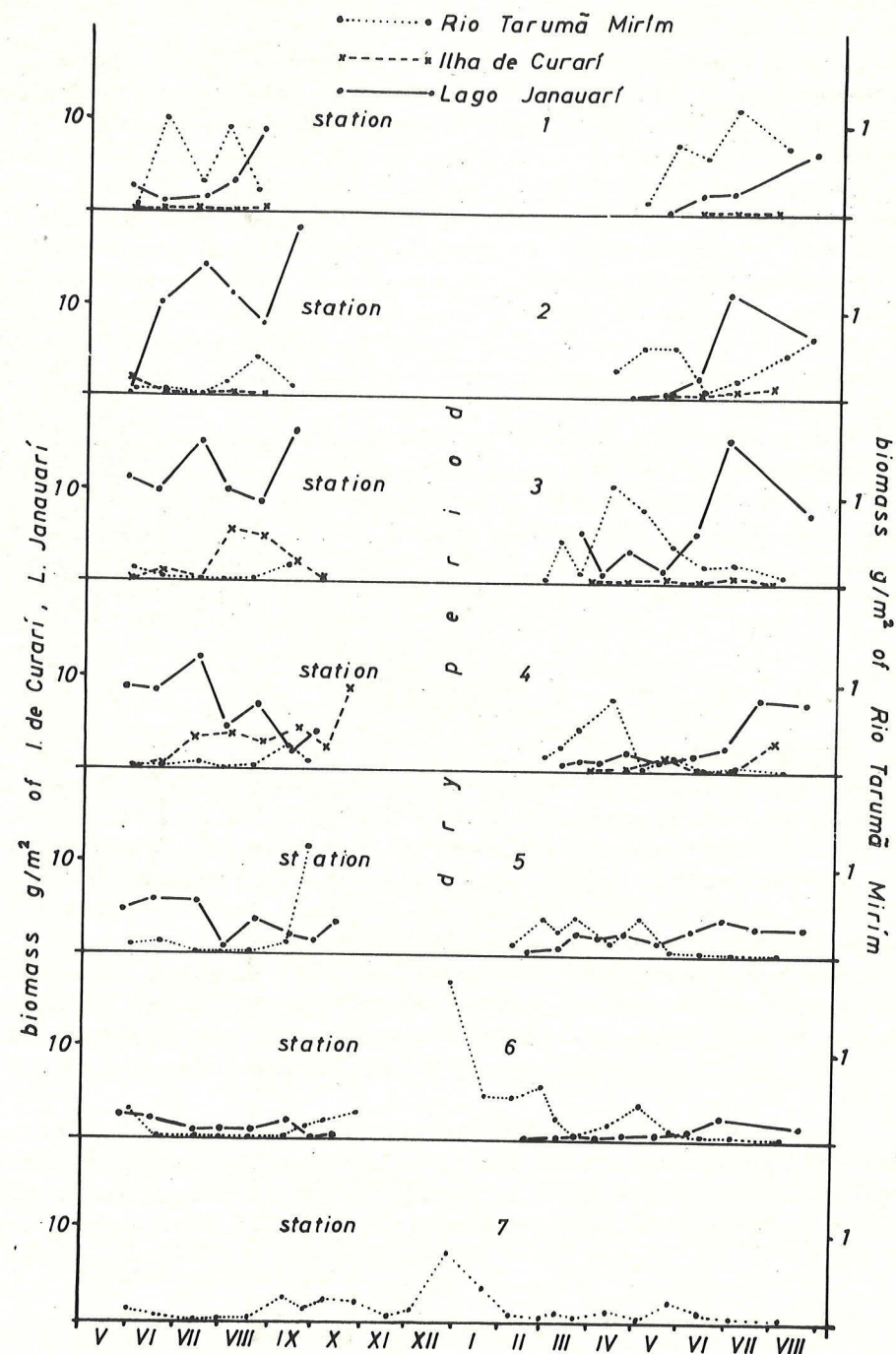


Fig. 17: The periodicity of the biomass on Ilha de Curarí, Lago Janauarí, and Rio Tarumã Mirim.

taking into account its number of individuals was considered. Previously mentioned difficulties (see chapter 4.3.4.) with *Campsurus notatus* occur and as they could not be solved clearly, two values will be given, a hypothetical one calculated according to ALLEN (1951) and one actually determined. The hypothetical production of *Campsurus notatus* amounted to 4.3 g/m^2 per year and the determined production to 2.6 g/m^2 per year for sampling stations 3 and 4. Of this production probably 0.15 g/m^2 per year emigrates in form of young larvae in the 2nd generation. For *Pisidium sterkianum* a production of 2.6 g/m^2 per year was calculated for both generations. The estimation of the production of *Eupera si-moni* taking into account the young bivalves immigrated in the benthos at high water, amounts to $\pm 0.9 \text{ g/m}^2$ per year. The P/B quotients for the studied animals are the following: *Campsurus notatus* = 6, *Pisidium sterkianum* = 14. These estimates, therefore, lie within the range of values found in temperate zones.

The production of the important chironomids could not be studied. In an estimation of the total production, the more rapid development of smaller species must be taken into account. Using a P/B quotient of 10-20 as it is applied to the littoral area of lakes in the temperate zones, an annual production of $\pm 10\text{-}15 \text{ g/m}^2$ for sampling station 4, the area of the highest production, could be estimated. The production of other parts of the forest lies well below that value.

5. Lago Janauari

5.1. General description

The Lago Janauari lies on the opposite shore from Manaus on the spit between the Rio Negro and the Amazonas-Solimões (quadrat 2 in Fig. 2). This inundation forest is divided from the Rio Solimões by a terra-firme wall. Whilst white water flows through several channels into the forest during the high water period, black water enters the lake in a broad front from the Rio Negro. The chemistry of the water in the investigated areas is, therefore, influenced by the inflow of two different river types.

Six sampling stations were situated in the forest. No. 1, the highest, was nearest to the terra-firme wall. No. 6 lay immediately next to the lake (Fig. 18). The last station was dry from the end of October to the middle of January. In 1971 the maximum inundation was 7.70 m high. The highest lying station, No.1, had a maximum water level of $\pm 1.5 \text{ m}$ (Fig. 19).

The following plants could be identified in this area: *Quina rhytidopus* TUL., *Cassia leiandra* BENTH., *Piranhea trifoliata* BAILL., *Vitex cymosa* BERT., *Inga* sp., *Pseudoxandra polyphleba* FRIES., *Paullinia* sp., *Ceiba pentandra* GAERTN., *Olmediophaena maxima* DUCKE, *Hevea spruceana* MUELL., *Buchenavia grandis* DUCKE, *Aspidosperma exelsum* BENTH.

5.2. Environmental factors

5.2.1. The substratum

During the inundation period, water of the Rio Amazonas-Solimões flows into the

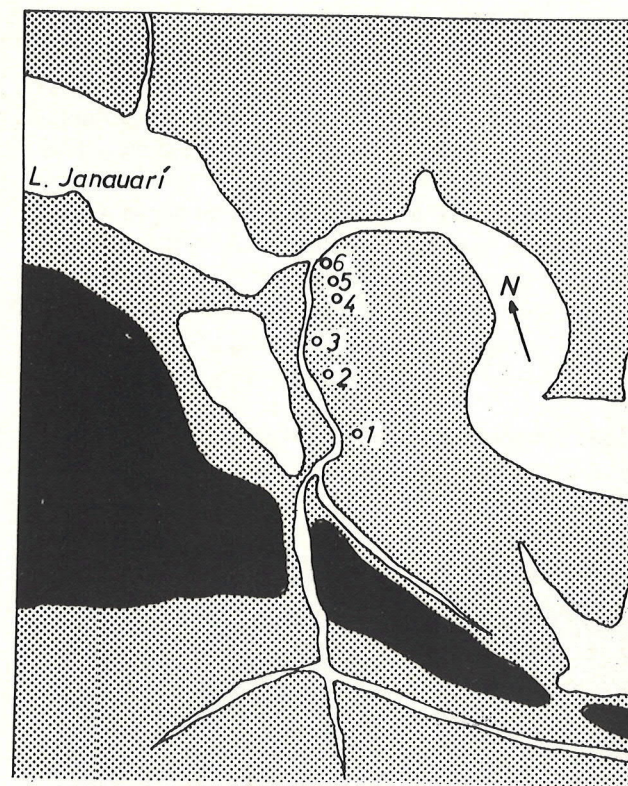


Fig. 18: The sampling area at Lago Janauari, showing the 6 sampling stations (terra firme - black, inundable area - grey).

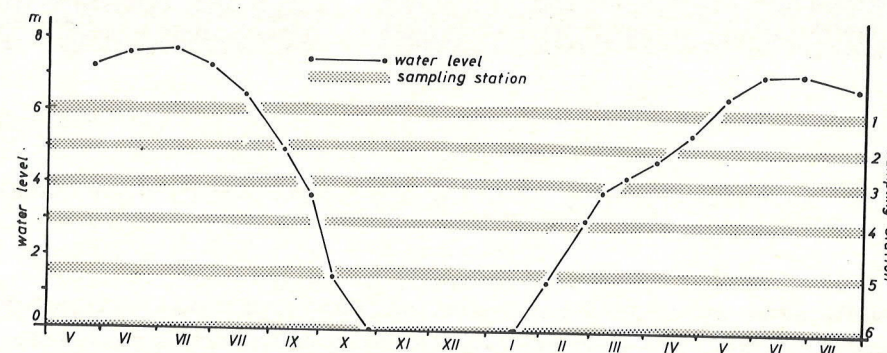


Fig. 19: The 6 sampling stations at Lago Janauari according to the water level fluctuation and the inundation period.

forest. The sediments, carried by the inflowing water, influence the structure of the substratum on deposition. The water entering the várzea loses its sediment load fairly rapidly.

In lower Amazonia, in the Canal do Piapo 83.72 % of the sediment load was deposited over a distance of ± 400 m during the high water period. In addition, the particle size fell from 0.2 mm diameter to 0.06 mm diameter over this distance. Only a fraction of the total sediment load of the Amazon river could be found at an area lying some distance from the river. The organic fraction of the sediment load increases correspondingly with distance from the main river (SIOLI 1951 a, 1957).

The suspended material supply differs during the course of one year depending on the strong influence of the two different river types. At sampling station 6 the inflow of the two water types could be detected by transparency measurements (Fig. 21). With the beginning inundation, white water inflow predominated. At this time transparency amounted only to 0.4 m. During the high water period the transparency remained constant. At the end of the inundation transparency increased rapidly, corresponding with a strong inflow of black water.

In the inundation forest at Lago Janauari the suspended material load of the inflowing water was too small to entirely cover the existing litter layer. Only a thin sediment layer covered the litter (Fig. 20). In the dry period, up to the beginning of the inundation,

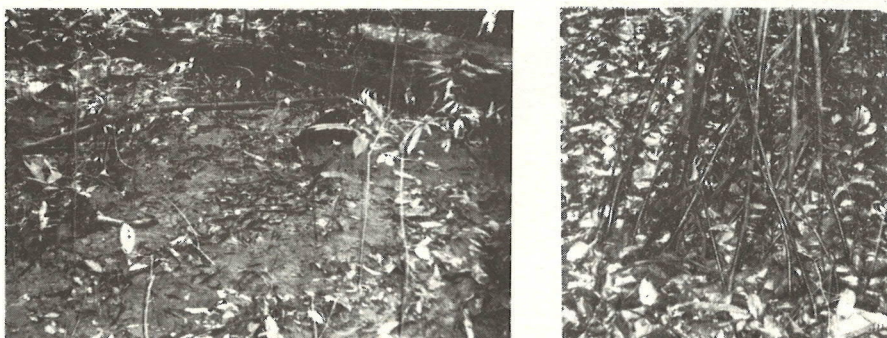


Fig. 20: Soil surface of sampling station 5 at Lago Janauari (a) and of station 2 at Rio Tarumã Mirim (b).

± 5.4 t/ha average dry weight of litter covered the ground. Particle size of the sediments was studied at stations 4 and 6. It shows that clay sediments of 2μ diameter predominate. The clay material, on drying, aggregates to form large particles however. These could not be broken down by the particle size analysis as reflected by the high coarse particle values.

5.2.2. Conductivity

In mixed-water areas the chemistry of the water body depends on complicated processes which are always different in the different areas, and which must be separately described for each area (GESSNER 1960 a, FITTKAU et al. 1975).

The Lago Janauari obtains white water through several channels. The lake itself seems to have a strong inflow of black water during the low water period. With the beginning of inundation, the conductivity in the lake was only $13.7 \mu S_{20}/cm$. The inflow of white water then increased rapidly. Therefore the conductivity of the water, entering into the forest rose to $28.0 \mu S_{20}/cm$. Up to the beginning of March, a further increase in the conductivity to $55.9 \mu S_{20}/cm$ was observed (Fig. 21).

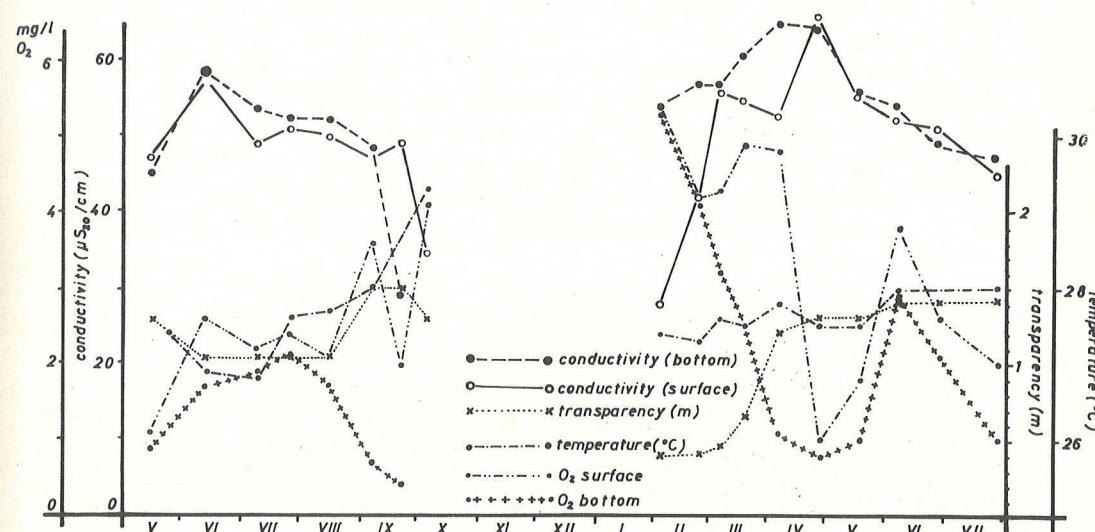


Fig. 21 : Conductivity and oxygen concentration of surface and bottom water, transparency, and temperature of the bottom water of station 6 at Lago Janauari.

The different values of the conductivity between the surface and the deep water suggest a stratification between the inflowing white water along the bottom and the black water remaining at the surface. As the two water bodies mixed further, the conductivity at the surface increased. At the same time the transparency increased, because the sediment load decreased due to further mixture with black water.

Later a new stratification developed. Electrolyte rich water lay in the deepest part (Fig. 22). The temperature between surface and deep water showed a maximum difference of only $1^{\circ}C$ (see chapter 6.2.3.). Therefore, the density stratification is assumed to depend partly on the chemical conditions, i.e. on the different concentrations of electrolytes, and on the sediment load of the two water bodies.

The rapid increase of the conductivity at the surface at the beginning of May may be explained by the strong inflow of white water which flowed over the river levee at this time. This results in complete mixing of the two water types. The period following this showed a continuous decrease in the conductivity depending on a greater inflow of black water. During this period stratification occurred either to a limited extent or not at all.

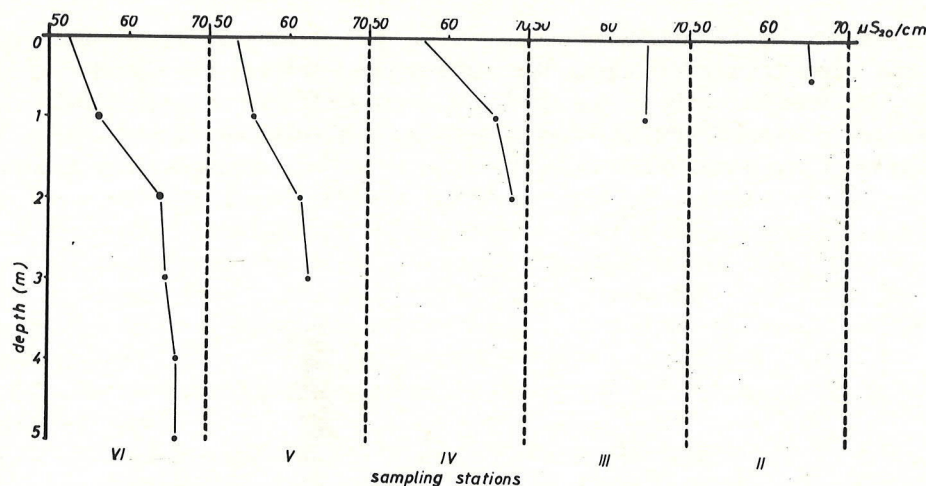


Fig. 22: Vertical stratification of conductivity on 6-4-1972 at Lago Janauari.

5.2.3. Oxygen

Similar to the conditions in the inundation forest on Ilha de Curari, conductivity and oxygen concentration seem to be correlated with different factors. After equally high oxygen values of 4-5 mg/l in the deep and the surface water at the beginning of inundation, a stratification developed (Fig. 21). On one occasion, 4.8 mg/l O₂ were found at the surface, whereas the deep water contained only 1.1 mg/l O₂. This stratification terminated together with that of electrolyte rich and electrolyte poor water. Therefore, the breakdown of the two types of stratification is assumed to depend on the same causes (see chapter 5.2.2.). During the high water period oxygen concentration at the surface and in the deep water amounted to ± 2 mg/l O₂. At the end of the inundation period a new stratification developed.

GESSNER (1961) referred to the problem of the oxygen consumption due to the breakdown of the organic substances during the high water period in the inundation forest. A stratification with oxygen free deep water is not always formed by this process however, as is shown by an example in the inundation forest at Lago Janauari. In this case an oxygen consumption resulted an oxygen poor deep water. As the water level rose, however, the strong flow disturbed the existing stratification causing an increase of the oxygen concentration in the deep water. This process is of great biological importance. The oxygen concentration will become problematical if the speed of flow does not increase with rising water during a year with a low high water level. It can be assumed, that in this case the oxygen stratification will persist, thereby strongly influencing the benthos community.

The inundation period can be subdivided in the following phases:

1. Inflow of white water; increase of conductivity; decrease of the oxygen concentration in the deep water.
2. Relative stagnation of the white water inflow; stratification of electrolyte poor but oxygen rich water at the surface and electrolyte rich but oxygen poor water underneath.

3. Strong inflow of white water; end of the stratification; slow decrease of the conductivity and rapid increase of the oxygen values to a relatively constant value of ± 2 mg/l.
4. Falling water; slow followed by rapid decrease of the conductivity; new development of an oxygen stratification.

5.2.4. pH and temperature

In the inundation forest at Lago Janauari no relationship between pH and temperature and the water level fluctuations could be found (Fig. 21). With the beginning of inundation only the pH, with a value of 5.7, shows the strong black water influence on the surface water at this time. During the following inundation the values remained relatively constant about 6.4. Differences between surface and deep water could not be found. Both the temperature and the pH as well as the conductivity and oxygen concentration did not vary within the different parts of the forest. The temperature increase at the end of the inundation period may depend on the higher insolation during the dry season.

5.3. The macroinvertebrates of the benthos

5.3.1. The seasonal periodicity in the community composition

The inundation forest at Lago Janauari contains a richer fauna than the Ilha de Curari. Bivalvia, Gastropoda, Decapoda, Chironomidae, Oligochaeta, and Ephemeroptera are of some importance. The most important species of the above mentioned groups are: *Eupera simoni*, *E. bahiensis* (Bivalvia, Sphaeriidae), *Chironomus latistylus* and *Chir. sp. AR 4* (Diptera, Chironomidae), and *Brasilocaenis irmieri* (Ephemeroptera, Caenidae) (Table 4).

The benthos community showed a marked periodicity, being influenced obviously by the water level fluctuations. The first phase during rising water was extremely poor in terms of species (Fig. 23). In particular *Eupera simoni* inhabiting the forest during the whole year (see chapter 5.3.4.), *Brasilocaenis irmieri*, Cyprinae (Ostracoda) and Culicidae (Diptera) may be mentioned however. This first phase was also notable for the low abundances of the species. In the second phase of the rising water a strong production by different animal groups, particularly by *Opisthocysta flagellum* (Oligochaeta, Opisthocystidae), *Chironomus latistylus*, *Chir. sp. AR 4* and *Eupera simoni* began. During the high water *Eupera simoni*, *Brasilocaenis irmieri* and *Laevapex aguadae* attained their maximum abundance, while *Opisthocysta* and *Chironomus* were strongly reduced. The falling water was characterized by the rapid increase in abundance of *Aroapyrgus sp.* Correspondingly, the maximum abundance of *Eupera bahiensis* lay at the beginning of this phase. Although the seasonal abundance of the several species or animal groups differed, all the mentioned animals were fairly abundant during the whole year. The Culicidae alone, preferring the low flooded areas, were found only at the rising and falling water. In the inundation forest at Lago Janauari the periodicity does not depend on deteriorating living conditions as it does on Ilha de Curari.

5.3.2. The vertical stratification of the fauna

The vertical stratification of the fauna generally shows a more homogeneous distribution than on Ilha de Curari. It is remarkable that the sampling station 1 and 6 lying near the border of the forest in some respect differ from the rest. Thus, *Eupera simoni* has its optimal habitat at the stations 2-5 (Fig. 24). At the lower flooded station (1) it is replaced

Table 4: The differentiated taxa of the inundation forest at Lago Janauari (A - % of annual mean abundance, B - % annual mean biomass).

taxonomic group	%A	%B	taxonomic group	%A	%B
NEMATHELMINTHES			DECAPODA	0.1	5.2
Nematoda			<i>Euryrhynchus burchelli</i>		
			CALMAN		
PLATHELMINTHES			<i>Macrobrachium amazonicum</i>		
Turbellaria	2.0	0.2	HELLER		
			Brachyura		
MOLLUSCA			AMPHIPODA		
Bivalvia	41.4	80.8	Gammaridae		
<i>Pisidium sterkianum</i> PILSBRY			Insecta		
<i>Pisidium punctiferum</i> GUPPY			DIPTERA		
<i>Eupera simoni</i> JOUSSEAUME			Chironomidae	16.9	2.6
<i>Eupera bahiensis</i> SPIX			<i>Polypedilum</i>		
Gastropoda			<i>Chironomus latistylus</i>		
Ancylidae gen. sp.			REISS		
<i>Hebetancylus moricandi</i> D'ORB.			<i>Chironomus</i> sp. AR 4		
<i>Gundlachia bakeri</i> PILSBRY			<i>Stenochironomus</i>		
<i>Laevapex aguade</i> GOODRICH & v. d. SCHALIE			further Chironomini species		
<i>Littoridina pusilla</i> HAAS			Tanytarsini		
<i>Potamopyrgus latus</i> HAAS			Tanypodinae		
<i>Aroapyrgus</i> sp.			Orthocladinae		
<i>Ampullarius</i>			Culicidae		
Planorbidae			Ceratopogonidae		
			Chaoboridae		
ANNELIDA			TRICHOPTERA		
Oligochaeta	15.8	2.0	ODONATA	0.5	2.2
aff. <i>Aulophorus</i>			Anisoptera		
aff. <i>Dero</i>			Zygoptera		
<i>Opisthocysta flagellum</i> LEIDY			HETEROPTERA		
Tubificidae			<i>Tenagobia socialis</i> WHITE		
Hirudinea	1.1	0.6	COLEOPTERA		
			Dytiscidae		
			Gyrinidae		
ARTHROPODA			EPHEMEROPTERA	9.7	1.0
Acari			<i>Asthenopus amazonicus</i>		
Crustacea			HAGEN		
OSTRACODA			<i>Brasilocaenis irmleri</i>		
			PUTHZ		
			Ephemerellidae		
			Ephemeridae		

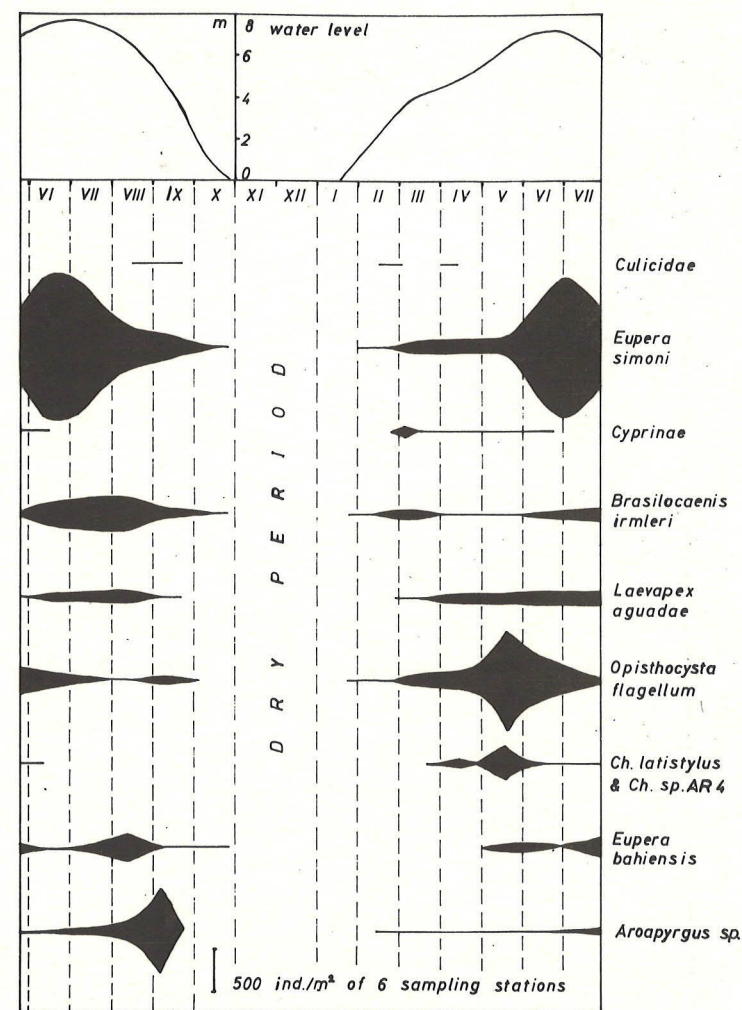


Fig. 23 : The annual distribution of different species compared with the water level fluctuations at Lago Janauari.

by *Eupera bahiensis*. At the deepest flooded station (6) *Eupera simoni* occurs, associated with *Eupera bahiensis*, only in low numbers. *Brasilocaenis irmleri* and *Opisthocysta flagellum* are similarly distributed, being concentrated in the center of the forest although not to the same extent as the bivalves (Fig. 25). *Brasilocaenis irmleri* occurs more in the deeper flooded areas of stations 4 and 5, whereas *Opisthocysta flagellum* prefers the stations 2-4.

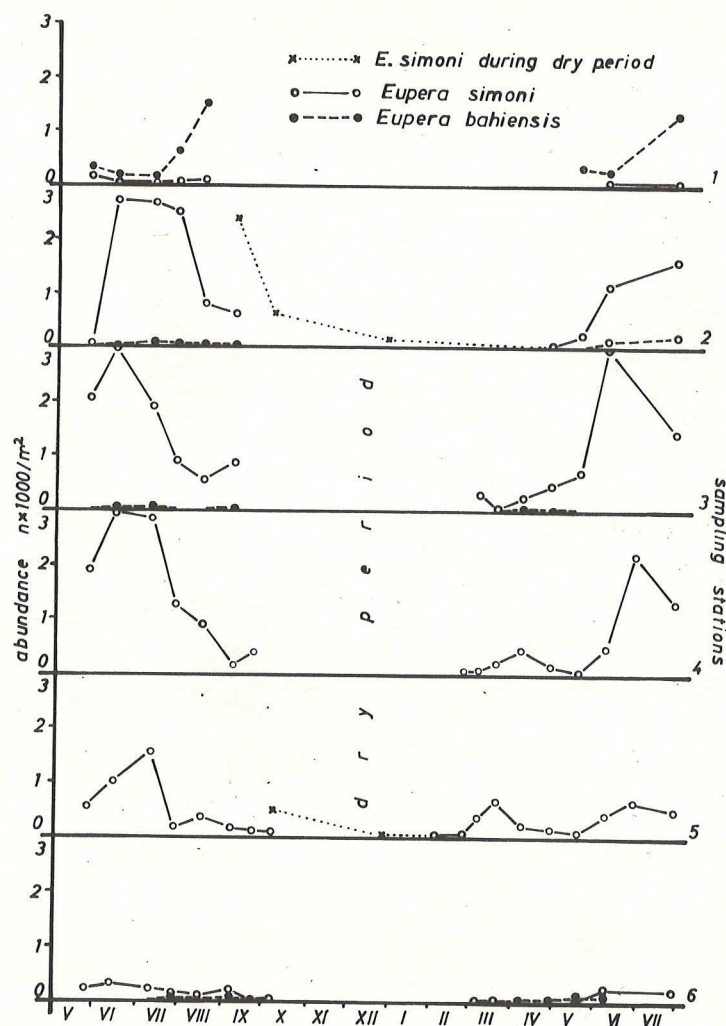


Fig. 24 : Distribution of *Eupera simoni* JOUSSEAUME and *Eupera bahiensis* SPIX and abundance decrease of *E. simoni* during the dry period of the stations 2 and 5.

The stations 2-5, therefore, may be considered as the optimal habitat for the benthos community of the inundation forest. This can be easily understood if the fauna is assumed to be adapted to a forest biotope (see chapter 4.3.3. and 5.3.3.). The edges of the forest are naturally influenced by the neighbouring areas to a greater extent than the center. At station 6 the influence of the lake and at station 1 the terrestrial influence may be responsible for the different community composition.

Fig. 24 and 25 show the vertical stratification of the different phases in water level fluctuation distributed on the following stations (see chapter 5.3.1.).

1. rising water - station 4-6 - *Eupera simoni*, *Brasilocaenis irmleri*, Cyprinae, Culicidae;
2. rising water - station 1-6 - *Opisthocysta flagellum*, *Chironomus latistylus*, *Chir. sp. AR 4*, *Eupera simoni* (in low abundance);
3. high water - station 1-6 - *Eupera simoni*, *E. bahiensis*, *Brasilocaenis irmleri*, *Laevapex aguadae*;
4. falling water - station (1) 2-6 - *Eupera simoni*, *E. bahiensis*, *Brasilocaenis irmleri*, *Aroapyrgus sp.*

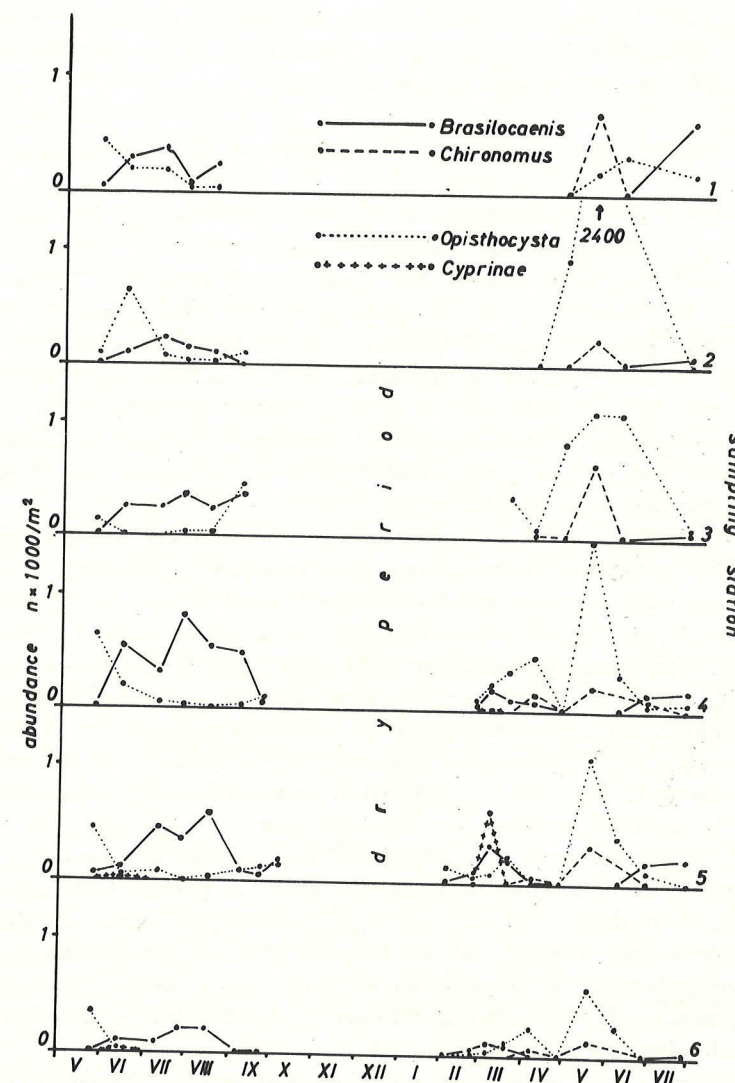


Fig. 25 : Distribution of *Brasilocaenis irmleri* PUTHZ, *Chironomus latistylus* REISS and *Chir. sp. AR 4*, *Opisthocysta flagellum* LEIDY and Cyprinae at Lago Janauari.

The first phase, containing *Brasiloacaenis irmleri* in its community, attracts attention, because this phase is not found at the later flooded stations. Those stations begin with the community of the second phase in which *Opisthocysta flagellum* and *Chironomus latistylus* predominate. This phenomenon cannot be explained. Perhaps competition with the animals of the second phase is important, particularly, as *Brasiloacaenis irmleri* seems to prefer the stations 4 and 5 from which it is displaced by an oxygen deficit (see chapter 5.3.3.).

The second phase is of greater extent in the areas flooded for longer time periods. Thus, the minimum abundance of *Eupera simoni* of the second phase is more marked in the deep lying areas. The production of *Opisthocysta flagellum* increases more slowly in the deep lying areas than it does at the higher lying stations. The maximum abundance however, is reached at the same time at all stations.

5.3.3. The most important factors influencing the periodicity and the stratification of the fauna.

pH and temperature do not seem to be of great importance in influencing the periodicity of the benthos community. The electrolyte and oxygen concentrations, with strong fluctuations within one year may, however, explain the periodicity of the fauna. In particular the severe oxygen deficit in the deep water during the months April/May may be of a great importance. The changing phases in water level during this time are worth noting. Whereas in the first phase with decreasing oxygen concentration, *Eupera simoni*, *Brasiloacaenis irmleri* and Cyprinidae predominated, in the following months April/May *Chironomus latistylus*, *Chir. sp. AR 4*, and *Opisthocysta flagellum* were found. Both *Chironomus* and *Opisthocysta* have posterior gills (CERNOSVITOV 1936, MARCUS 1944) which would be an advantage in oxygen poor water.

Opisthocysta flagellum had a conspicuous distribution. At the deeper lying stations it disappeared at the time of the lowest oxygen concentration, but reappeared in the following sample, when a small oxygen increase was recorded (Fig. 26). This disappearance of *Opisthocysta flagellum* at 27-4-72 cannot be explained merely by methodological error, particularly as it disappears simultaneously at the three deeper lying stations (4-6) (Fig. 25). The distribution of this Oligochaete may depend on the oxygen deficit of the deep water. The limiting oxygen concentration of the water is to be assumed to be about 1 mg/l in this area for *Opisthocysta flagellum*. The rapid disappearance and new reappearance of *Opisthocysta flagellum* can hardly be explained by reproduction, even rapid reproduction by budding. The rapid reappearance may therefore depend on migrations up and down the trees. Such migrations are also found in the related Naididae (see chapter 6.3.2.).

The structure of the substratum cannot be regarded as an important limiting factor for the distribution of the benthos community, as it is developed similarly in all parts of the forest as a litter-layer. The very uniform structure of the substratum may be a reason for the uniform distribution of the benthos community. Nevertheless the amount of litter is not homogeneous everywhere. Thus an interdependence between the population density and the litter development exists.

Fig. 27 shows the relation between the litter weight and the biomass of *Eupera simoni*. The correlation coefficient could be calculated by the logarithmic values. It amounts to 0.871. This is significant at the level $p < 1\%$. Correspondingly the population density in $B \text{ g/m}^2$ depends on the litter amount with 75,9 % (see chapter 4.3.3. and 5.3.5.).

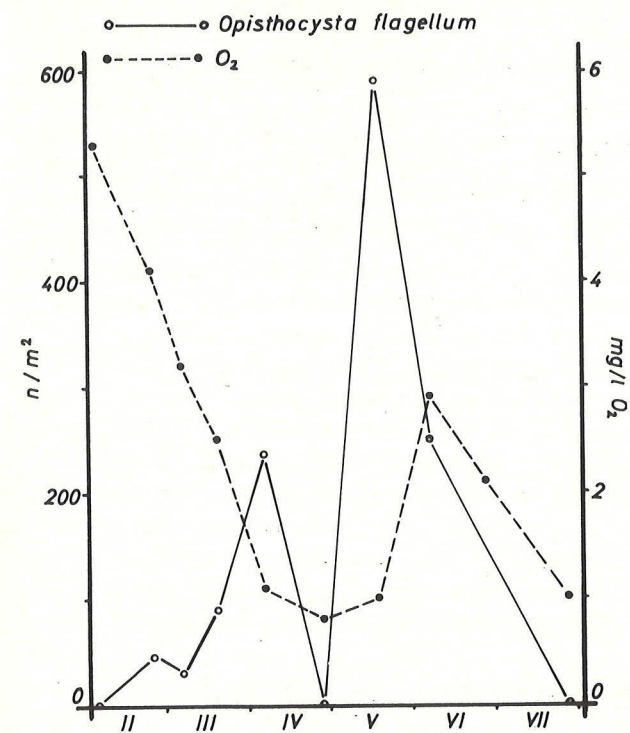


Fig. 26: Distribution of *Opisthocysta flagellum* LEIDY compared with the oxygen concentration of the bottom water of station 6 at Lago Januari.

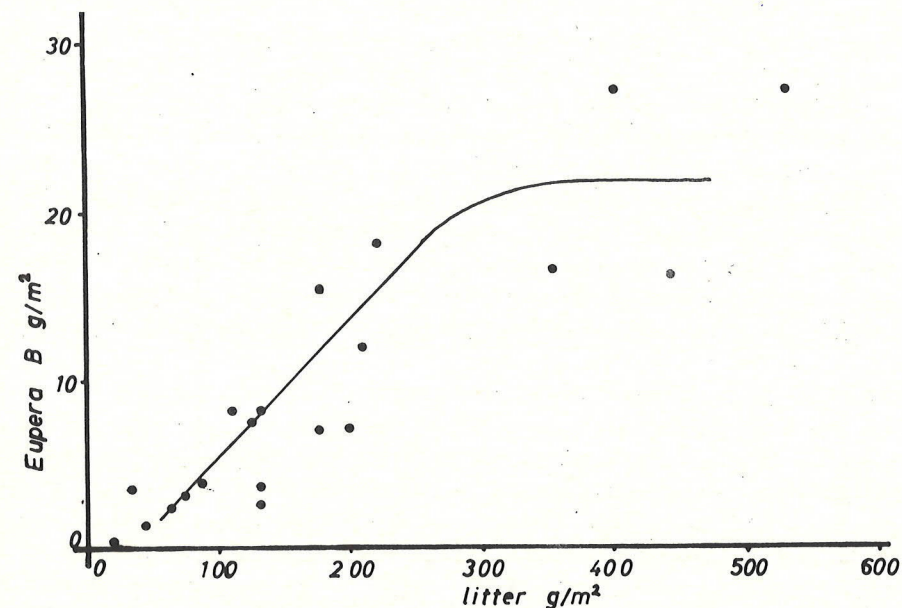


Fig. 27: Biomass (g/m^2) of *Eupera simoni* JOUSSEAUME in relationship to litter weight (g/m^2) of station 3 at Lago Januari.

5.3.4. Population-dynamics of *Eupera simoni*, *Eupera bahiensis* and *Chironomus latistylus*.

Eupera simoni

An interesting adaptation to the particular ecological conditions of the inundation forest was detected for *Eupera simoni*. This bivalve persisted in the forest during the dry period. This accounts for many of the population-dynamic phenomenon of this species.

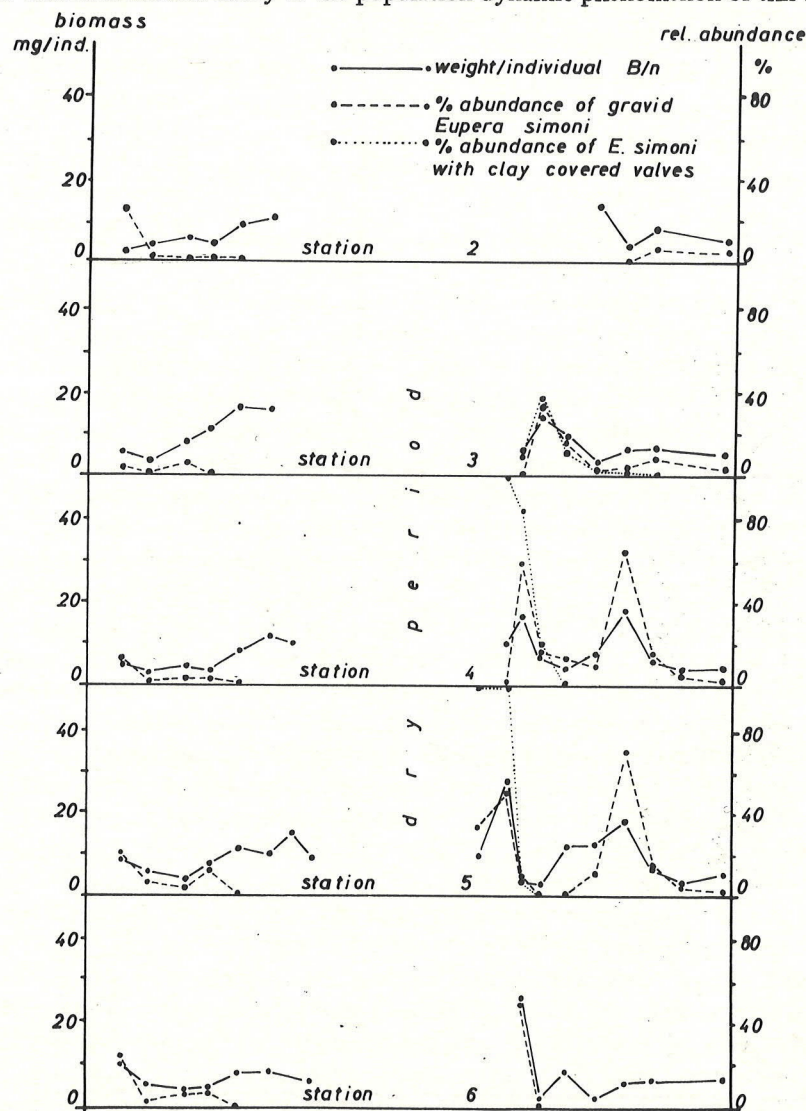


Fig. 28 : Periodicity of the mean individual weight of *Eupera simoni* JOUSSEAUME compared with the relative abundance of the gravid bivalves and relative abundance at rising water of those specimens of *Eupera simoni* which persisted in the inundation forest during the dry period.

As has already been shown in Fig. 24, this bivalve has two production phases at the deeper lying stations 4 and 5, whereas at the remainder of the stations only one phase could be observed. The growth periodicity of the bivalve during one year shows the two generations, produced during the inundation period (Fig. 28). Semiadult animals grow rapidly at the beginning of the inundation. In March the first young bivalves appear, becoming adults of the second generation by April/May. The first generation can be recognized clearly only at the stations 4 and 5. The populations of the stations 6 and 3 seem to be heterogeneous in this respect, probably caused by a mixed population of different generations.

The population structure with animals of different generations must be viewed in connexion with the rising water. Because not all parts of the forest are simultaneously flooded, the growth phases of the bivalve population should differ in the different parts of the forest. Thus, in April/May it is possible that stations 2,3, and 6 may be simultaneously inhabited by very young bivalves of the second generation from the stations 4 and 5, and adults of the first generation. At the higher lying station 2 there is not enough time to allow the development of two generations. The beginning of the third generation, which in fact will be the first generation of the next year, starts in June. The animals of this generation cannot grow to adult stage but finish growing in August, the time of rapidly falling water.

These successive generations can be easily illustrated by the distribution of gravid animals (Fig. 28). The maximum abundance of gravid animals occurs in February and May/June. The populations at the stations 4 and 5 contain 50-70 % gravid bivalves at this time, whereas at the stations 2,3, and 6 only a small abundance of gravid adults was obtained. This also indicates that the individuals making up these populations are largely the young animals which have immigrated here from stations 4 and 5.

As was mentioned previously, the semiadult animals of the first generation persist in the forest during the dry period. These bivalves can be recognized by their old clay covered valves. Naturally at the beginning of the inundation period their contribution to the total population was 100 % (Fig. 28). After the production of young bivalves in February the relative abundance of these animals decreases. It is interesting that at station 3, the abundance of bivalves which survive the dry period in the forest does not make up 100 % of the total population however. This phenomenon can only be explained by the immigration of young bivalves. Dispersal at least of young bivalves can therefore be assumed with *Eupera simoni*.

A migration ahead of the falling water to avoid remaining on dry land was not detected. Therefore the effects of the dry period on the bivalve population were investigated experimentally. Samples collected during the dry period show a strong decrease of the bivalves (Fig. 24). This decrease occurs particularly in the first part of the dry period. Depending on the extent of the dry period in the different parts of the forest, a varying number of individuals die. Thus, at station 2 virtually no animal survived up to the beginning of the next inundation from an original population of 2400 n/m², whereas at station 5 there were some animals which were able to survive and develop the new population.

This reaction to dryness was investigated experimentally. In four different cultures 30-40 individuals of *Eupera simoni* were subjected to 4 treatments: in water; in a non-climatic room with ± 80 % humidity; in a climatic laboratory with ± 60 % humidity; and above

silicagel for a time period of 4 months (from 6-10-71 till 5-2-72) (Fig. 29). The results showed that *Eupera simoni* survived in greater numbers in the water than in the drier cultures.

The same result was obtained by analysing the reproduction ratio of those animals which survived the dry conditions during the experiment. The surviving animals were then kept in water from 5-2-72. In the first week of March the newly hatched young bivalves were counted (Fig. 29). The population which had been kept in water since the beginning of the experiment had the highest reproduction ratio.

This experiment helps to explain a phenomenon which was noticed in studies on growth periodicity of *Eupera simoni* (Fig. 28). The animals of the first generation stop their growth in August even though they stay in the water till October. This growth stagnation indicates an endogen dormant stage. The experiment described above confirms this premise because those animals which were kept permanently in water produced young bivalves at the same time as those which were kept in dry conditions. The dormant stage of *Eupera simoni* seems to be a true diapause stage which may be followed in nature by a quiescence. The diapause stage occurs from August till February. After this, those bivalves which have to withstand dry conditions in higher lying areas until the inundation begins pass into a quiescent stage.

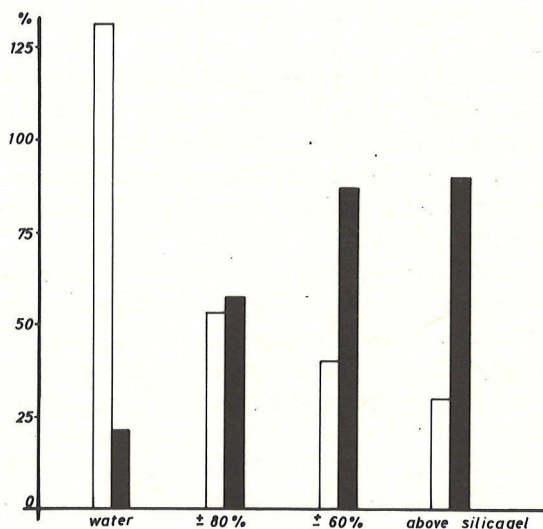


Fig. 29: The black columns indicate percentage of specimens of *Eupera simoni* JOUSSEAUME died during four months in four different cultures (mortality). The animals which survived this stress test were kept in water. The hatched young bivalves were counted after one month (white columns percentage of hatched young bivalves in correlation to adults which survived the stress test).

The induction of this diapause stage could not be studied further. It is a significant problem in the tropics where a number of environmental factors remain fairly constant throughout the year. A diapause stage, induced by the photoperiodism or the light conditions such as that found in insects in temperate zones, cannot operate in the tropics where daylengths are more or less constant. Similarly temperature, which also hardly fluctuates, can be neglected. Dryness however, must be regarded as an important factor. A similar diapause - quiescence correlation has been found in grasshoppers of the species *Locustana pardalina* (MATTHE 1951). On the other hand, nutrition may induce the diapause development as was detected for *Leptinotarsa decemlineata* (LARCZENKO 1957).

Eupera simoni grows from ± 0.1 mg at birth to 25-30 mg at adult stage. The generation time differs between the first and second generations. The length of the second generation amounts to 2 1/2 months. Natality fluctuates markedly within one year. During the main production periods in March and May/June 40 young bivalves/gravid ind. were found. At the same time natality decreased to 20 young bivalves/gravid ind. The number of young bivalves/gravid ind. was obtained by counting the young bivalves in the gill bags of the gravid adults. Therefore during this period, the decrease of young bivalves/gravid ind. may be affected by the successive birth of young bivalves.

As was shown in Fig. 29 dryness influences the natality in the diapause generation. The fertility also differs markedly in the two generations (Fig. 30). At the beginning of the inundation period the fertility of the first generation having a small abundance must be lower than in the second generation having a high abundance of gravid bivalves. The areas in which the main reproduction was obtained lay at the stations 3 and 4. At the station 2 a higher reproduction was observed in 1972 after a year of low reproduction ratio in 1971. This may be caused by the successive extraordinary high-waters which favour this area for *Eupera simoni*.

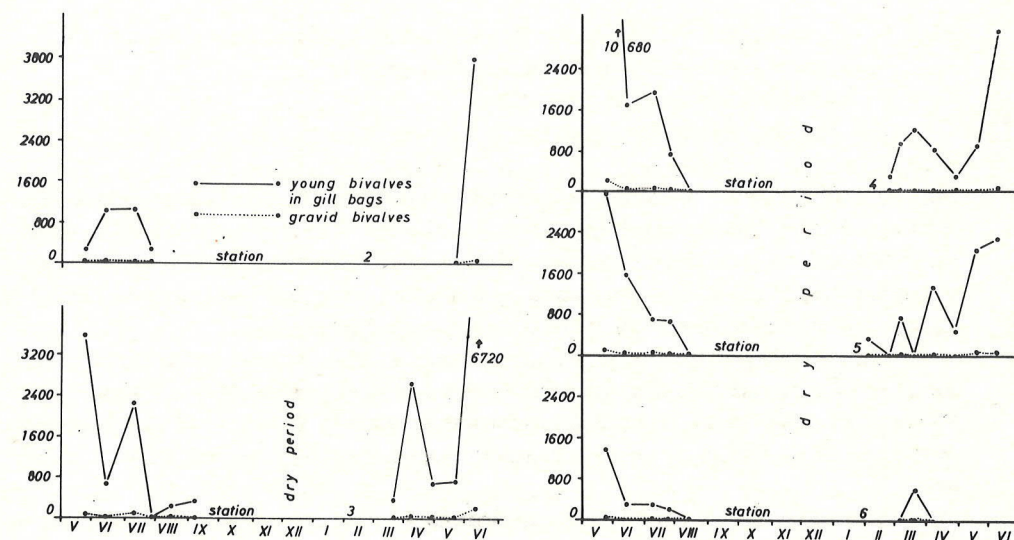


Fig. 30: Abundance (n/m^2) of gravid *Eupera simoni* JOUSSEAUME compared with the number of young bivalves found in the gill bags of the gravid animals to show the fertility of this bivalve population.

The dispersal of *Eupera simoni* within the forest complicates the estimation of the survivorship. The mean survivorship ratio of both generations is shown in Fig. 31 (a). Those animals had to be neglected which leaved the forest. Furthermore a survivorship ratio differentiated between the two generations was difficult to estimate because mixed populations between the first and the second generation existed at the higher lying stations.

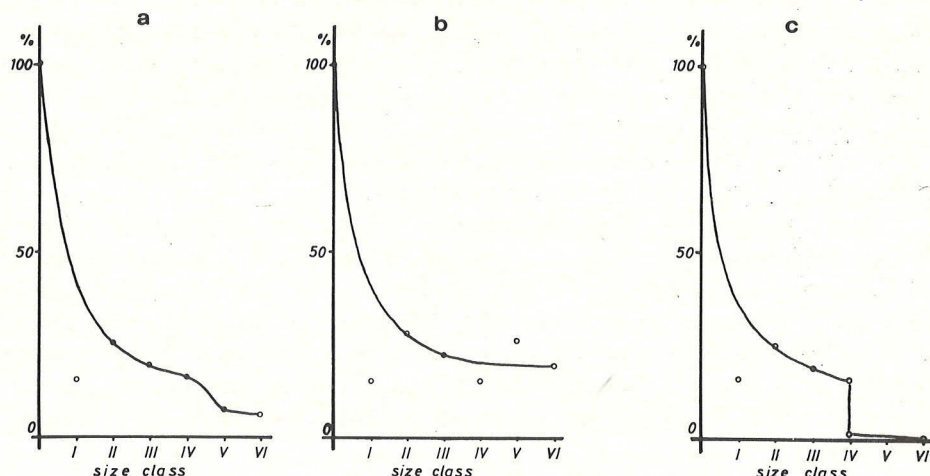


Fig. 31: Survivorship ratio of *Eupera simoni* JOUSSEAUME at Lago Janauari
a) mean survivorship ratio of generation I and II
b) survivorship ratio of generation II
c) survivorship ratio of generation I

But this problem could be solved, because the adults of the first generation could be differentiated from those of the second generation by their old clay covered valves. At the stations 4 and 5 a clear division between the animals of the first generation and the growing young bivalves of the second generation was observed, whereas at the stations 2 and 3 an exact coordination to one of the generations could only be assumed.

The mortality of the first generation persisting the dry period in the forest was found to be particularly higher than that of the second generation (Fig. 31 b and c). Whereas the mortality of the second generation amounts to 80 % that of the first generation was 98 %. The high mortality of the first generation may be affected by the dryness.

Because in the dry period many bivalves have to die, the abundance of the diapause animals has to be extraordinary high. Therefore two generations during the inundation period are necessary for *Eupera simoni*. The small abundance of gravid animals in the first generation only results an unimportant abundance increment. On the other hand the mortality being relatively low causes a high abundance of gravid bivalves in the second generation which produces a high population density in the next diapause generation.

Fig. 32 shows the interdependence of some environmental and biological factors involved in the population-dynamics of *Eupera simoni* in the inundation forest. The fluctuation between inundation and dryness are the most important factors which induce many environmental conditions influencing directly the abundance of *Eupera simoni*. In addition to the chemical conditions of the water body the sedimentation its effect on the substratum and its detritus particles as nourishment, is an important environmental factor (see chapter 4.3.3., 5.3.3., 5.3.5.) (IRMLER 1975). Dispersal and the fluctuation of the mortality and fertility are important biological factors.

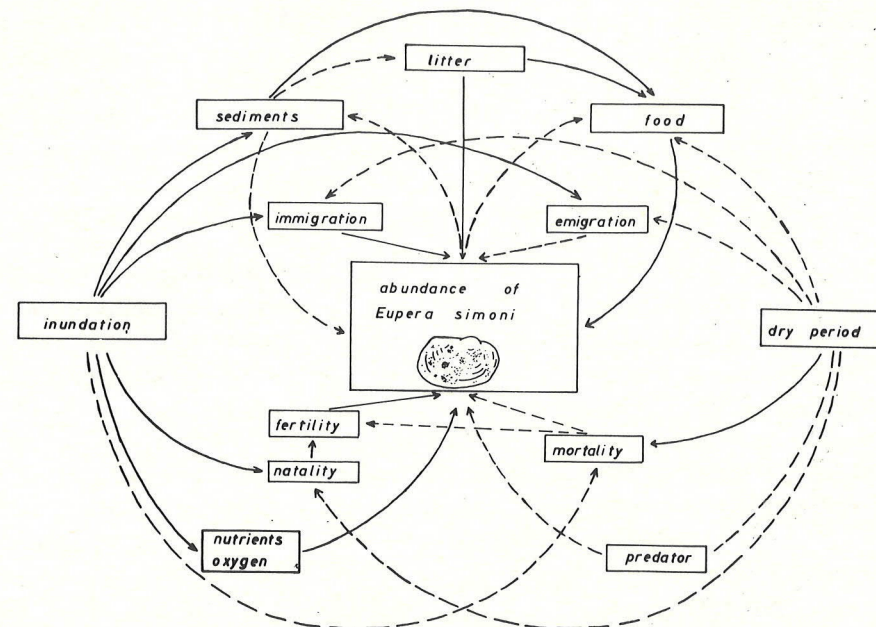


Fig. 32: Influence of inundation and dry period on a population of *Eupera simoni* JOUSSEAUME (continuous line - positive influence, broken line - negative influence).

Eupera bahiensis

Eupera bahiensis, the second important bivalve of the investigated forest, occurs particularly at the station 1 (Fig. 24). By this fact a higher tolerance of dryness was assumed for this species. The thicker valves of *Eupera bahiensis* attract attention (Fig. 33). 12 individuals with a mean valve length of 3.5 mm have a mean valve thickness of 0.11 mm, whereas *Eupera simoni* with a mean valve length of 4.8 mm has a mean valve thickness of 0.08 mm. It may be assumed therefore that *Eupera bahiensis* has a better shelter against dryness by its thicker valves than *Eupera simoni*. Competition to *Eupera simoni* may cause this retreat in areas, where *Eupera simoni* finds no favourable living conditions.

As a result of the short inundation *Eupera bahiensis* can produce probably only one generation at station 1 (Fig. 34). The short observation period avoids a more exact study of the development. At the end of the inundation 1971 semiadults seem to predominate. At the beginning inundation 1972 particularly adults and young bivalves occur. It may be assumed that bivalves, which survived the dry phase, produce young bivalves in this time. Whether *Eupera bahiensis* has a similar development as *Eupera simoni*, cannot be decided clearly.

The development of one generation amounts to 2-2 1/2 months. The mean natality lies at ± 33 young bivalves/gravid ind.. The growth occurs within the range of 0.1-13 mg. Thus, *Eupera bahiensis* is only half-weight of *Eupera simoni*. The mortality of *Eupera bahiensis* during the dry period, being lower than that of *Eupera simoni*, amounts to 85%

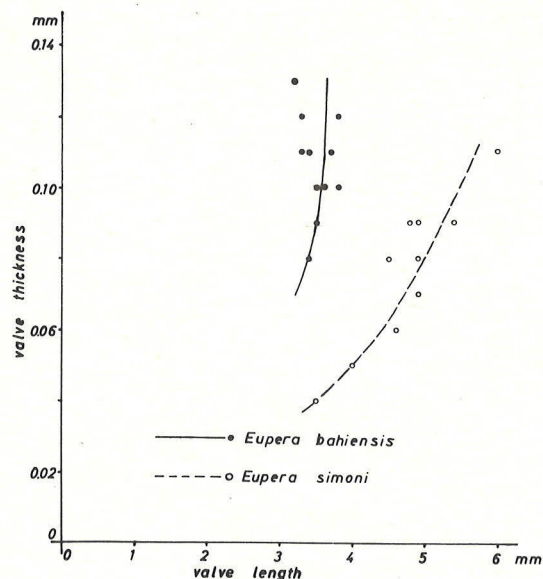


Fig. 33: Correlation of valve thickness and valve length for *Eupera bahiensis* SPIX and *Eupera simoni* JOUSSEAUME.

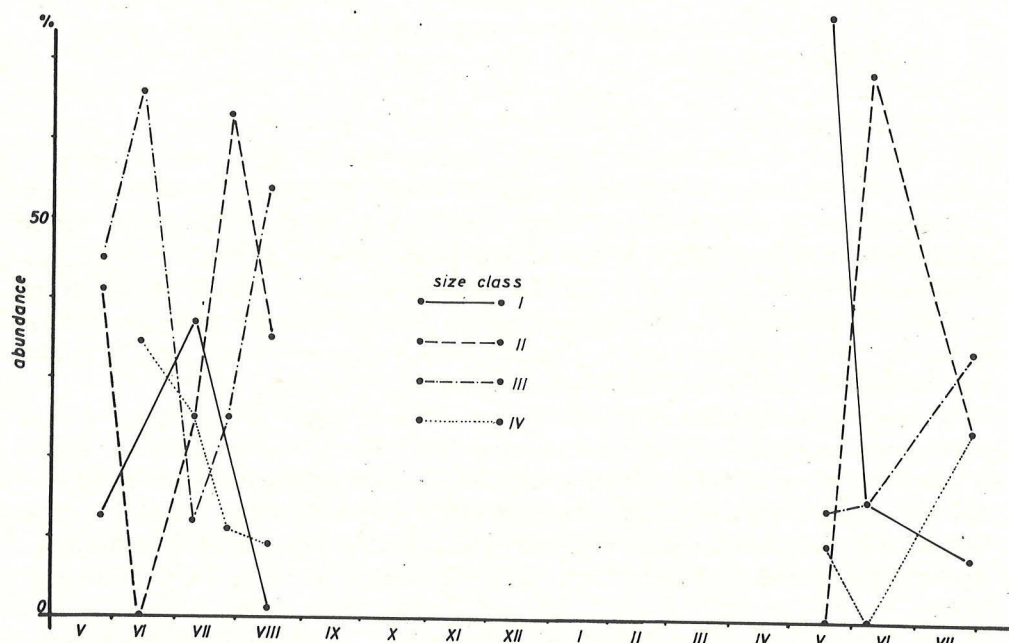


Fig. 34: Distribution of the four size classes of *Eupera bahiensis* SPIX of station one at Lago Janauari.

in spite of the long dry period. The low fertility in comparing to *Eupera simoni* seems to be compensated by a higher tolerance against dryness and lower mortality.

Chironomus latistylus

This chironomid species predominate in the months April/May in the benthos community. It is smaller than the *Chironomus gigas* in the inundation forest on Ilha de Curari (REISS 1974). Its growth increment amounts to 6-8 mg/ind.

5.3.5. Feeding habits

Corresponding to the physical-chemical conditions, the trophic factors changed according to those on Ilha de Curari. Tab. 5 shows the diet of the different animal groups. Besides the high number of detritivores the abundance of fungivores attracts attention (Fig. 15). Nearly 90 % of the fauna contain at least a small amount of fungi in their intestines. Animals with an intestinal content of leaf fragments could not be found as frequently as on Ilha de Curari. To these groups Gastropoda and Chironomidae have to be counted. Algae, also, were only found in low abundance in the intestinal contents. The predators predominantly feed on chironomids, Ostracoda and Opisthocystidae.

Table 5 : The composition of the intestinal content of different taxa at Lago Janauari.

Detritivores	
<i>Eupera</i>	: mainly - small detritus particles less - fungi, algae
Caenidae	: mainly - small detritus particles, fungi less - algae, Cyclopidae
Naididae and Opisthocystidae	: mainly - small detritus particles, fungi less - algae
Ancylidae	: fungi, small detritus particles
Hydrobiidae	: fungi, detritus, leaf fragments
Chironomini	: mainly - detritus and leaf fragments, pollen less - fungi
Tanytarsini	: detritus, fungi
Predators	
Tanypodinae	: Chironomini, Ostracoda, Naididae, Opisthocystidae
Anisoptera	: Chironomidae, Ostracoda, Naididae, Opisthocystidae
<i>Euryrhynchus</i>	: Naididae, Opisthocystidae
Ceratopogonidae	: probably haemolymph of chironomids

The breakdown of the litter is assumingly similar to that in the terra firme rain forest (STARK 1969), that means predominantly by fungi, whereas the fauna is only partly involved (see chapter 7.2). A great part of the soil invertebrates must be regarded as fungivores.

The importance of the leaf litter on the growth of *Eupera simoni* was examined in

three cultures (Fig. 35). 20 bivalves each were cultivated without leaf litter, with 2 g leaf litter, and with 20 g leaf litter. The washed leaves were put in a box with Amazon water. Then the mean weight increment/week was measured. This experiment resulted in a weight increase in the culture of 20 g leaf litter and a weight decrease in the other two cultures, showing the influence, directly or indirectly, of the leaf litter on the growth of *Eupera simoni*. It may be assumed that in nature *Eupera simoni* feed mainly on the detritus coming on with the current, because only a small weight increment could be obtained in the experiment. Dependence of the growth on the leaf supply was already detected for North-American insects in current waters (CUMMINS et al. 1973).

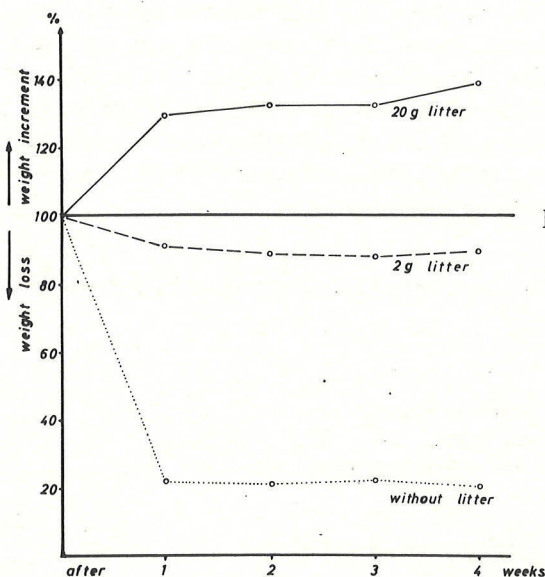


Fig. 35: Weight increment or weight loss of *Eupera simoni* JOUSSEAUME in three cultures with different litter weight. The original biomass of *Eupera simoni* for each culture was 100%.

Filtering rates of South-American Sphaeriidae are not published. Measurements on European *Sphaerium* species result in a dependence on temperature and the suspended solid concentration (HINZ & SCHEIL 1972, ALIMOV & BULION 1972). With decreasing suspended solid concentration the filtering rate increases. Due to *Eupera simoni* in the mixed water at Lago Janauari a higher filtering rate than on Ilha de Curarí can be supposed. According to the European data a filtering rate for *Eupera simoni* of $\pm 200 \text{ ml/m}^2$ and h can be estimated for the high water time with the maximum biomass of 10 g/m^2 . If the factor 4 (see chapter 3.2.) is taken into account the filtering rate increases to 800 ml/m^2 and h. Therefore, a relatively high influence of these bivalves on the suspended load content of the water may be suggested which perhaps contributes to the sediment deposition behind the river levee. SIOLI (1957) and SCHMIDT (1973) published data about the sediment load of decanted white water amounting to 25 mg/l respectively 6.8 mg/l . Estimating the influence of *Eupera simoni* on the suspended load, according to the mentioned data, $6\text{-}20 \text{ mg/m}^2$ and h of filtered suspended load was obtained.

5.3.6. Productivity

The distribution of the benthos fauna in the inundation forest at Lago Janauari is more homogeneous than on Ilha de Curarí. The highest biomass values occur in the center of the forest at stations 2, 3, and 4 (Fig. 17). They amount to 14.5 , 15.3 , and 12.2 g/m^2 . The lowest maximum biomass was obtained at station 6 with 2.6 g/m^2 . The mean annual biomass values of each station are the following: 1 = 2.8 g/m^2 , 2 = 7.4 g/m^2 , 3 = 7.4 g/m^2 , 4 = 4.3 g/m^2 , 5 = 2.7 g/m^2 , and 6 = 1.1 g/m^2 . If the highest value of the total annual biomass at station 3 amounts to 100 % at station 1 = 21,8 %, 2 = 73,2 %, 4 = 61,7 %, 5 = 45,2 %, and 6 = 15,4 % are obtained. The greatest part of the biomass has *Eupera simoni* with the following values in July 1971: 2 = 13.8 g/m^2 , 3 = 14.2 g/m^2 , and 4 = 11.8 g/m^2 . *Aroa-pyrgus* sp. as well has high biomass values of 11.4 g/m^2 at beginning September on the shoreline at station 2. With biomass values of molluscs always the weight of the valves have taken into account. The weight of the organic material lies well below those values particularly with bivalves where the water of the mantle cavity has to be subtracted. An estimation of the mantle cavity content of alcohol material results in the quotient of 1.7 of alcohol filled/empty bivalve.

Furthermore *Brasilocaenis irmleri* and *Opisthocysta flagellum* have to be mentioned, having maximum biomass values of 0.2 g/m^2 respectively 0.7 g/m^2 . The greatest part of the fauna has no influence on the productivity. Decapoda, having a considerable biomass/ind., are probably not caught quantitatively by the sampling methods. One individual of the *Brachyura* may weight already 0.6 g.

The production was again calculated according to the method described in chapter 4.3.6.. The following productions were obtained: *Eupera simoni* $\pm 30 \text{ g/m}^2$ and year, *Eupera bahiensis* = $\pm 18 \text{ g/m}^2$ and year. The production value of *Eupera simoni* being the mean production of the stations 2-6 may differ in the different parts of the forest according to the more favourable living conditions and the different long inundation. It may be lowest at the station 6, whereas at station 3 and 4 it may probably lie above the mentioned value. If the methodological error with the factor 4 described in chapter 3.2. and the quotient 1.7 for the water, enclosed in the mantle cavity, is taken into account a production of 70.6 g/m^2 and year is obtained for *Eupera simoni*. The P/B quotient of *Eupera simoni* amounts to 11.6; that of *Eupera bahiensis* to 6.4. If the rest of the fauna excluding the predators are included in the calculation with a P/B quotient of 10-20 a production of $90\text{-}110 \text{ g/m}^2$ and year is obtained.

These data, as well as those of the Ilha de Curarí, have to be regarded as rough estimations. Furthermore the animals of the inundation forest which depend on a firm substratum, in contrast to those of lakes, may inhabit also the trunks, branches, and leaves as it was detected for *Eupera simoni* and *Eupera bahiensis* (Fig. 36). The given values refer only to the benthically found animals. How much the production may increase by the inhabitation of the flooded trees, which enormously expand the living area, is unknown.

6. Tarumã Mirim

6.1. General description

The third investigated inundation forest lies at the lower course of the Rio Tarumã Mirim, near its mouth at the Rio Negro, about 20 km upstream from Manaus (quadrat 3



Fig. 36: *Eupera simoni* JOUSSEAUME on a trunk of a tree at Lago Janauari during the dry phase.

in Fig. 2). The water flows into the forest from the Rio Negro and particularly from the Rio Tarumã Mirim. In the forest were 7 sampling stations (Fig. 37). No. 1 was the highest, no. 7 the lowest lying station. The rest of the stations were successively between them. Part of the inundation forest at station 7 was covered by water during the year. At this place the lowest water level was 0.5 m, in 1971 the highest 8.3 m, while station 1 had a maximum inundation about 1.8 m (Fig. 44).

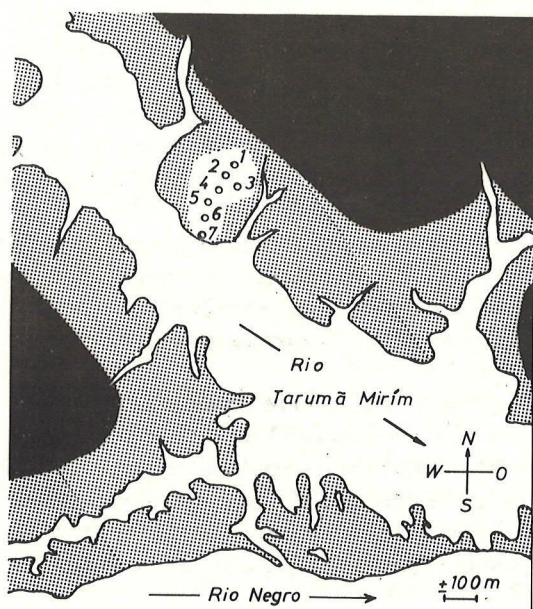


Fig. 37: The sampling area at Rio Tarumã Mirim showing the 7 sampling stations (terra firme - black; inundable area - grey).

The following plants of the forest were identified: in the lower lying area of the stations 7-5: *Jugastrum coriaceum* MIERs., *Remija* sp., *Salacia* sp., *Amanoa oblongifolia* MUELL., *Macrolobium acaciaefolium* BENTH., *Swartzia*, *Phyllanthus*, *Byrsonima*, *Nec-*

tandra amazonum NEES, and in the higher lying area (1-2): *Homalium pedicellatum* SPRUCE, *Aldina latifolia* BENTH., *Hevea spruceana* MUELL., *Aspidosperma excelsum* BENTH., *Anacampta rupicola* BENTH., *Swartzia polyphylla* DC.

6.2. Environmental factors

6.2.1. The substratum

Black waters only carry a neglectible suspended solid load. Therefore, in this inundation forest no sedimentation of inorganic suspended material occurs. The substratum consists of a litter layer (Fig. 20), which, at the end of the inundation, amounts to ± 18 t/ha and, at the beginning of inundation, to ± 9 t/ha (see chapter 7.2.).

From the great amount of humic matter carried by the black waters, one part precipitates and forms a gel-like cover on the litter layer. Till now continuous measurements of humic matters have been made in the Rio Prêto da Eva. There the humic matters fluctuates between 7 and 13 mg/l within one year. A periodicity could not be detected (MENEZES SANTOS et al. 1971). SCHMIDT (1972 a) published a value of 5.4 mg/l humic matter for the Tarumãzinho, lying in the same area as the Rio Tarumã Mirim. The transparency fluctuations within one year may indicate the humic matter concentration (Fig. 38). The

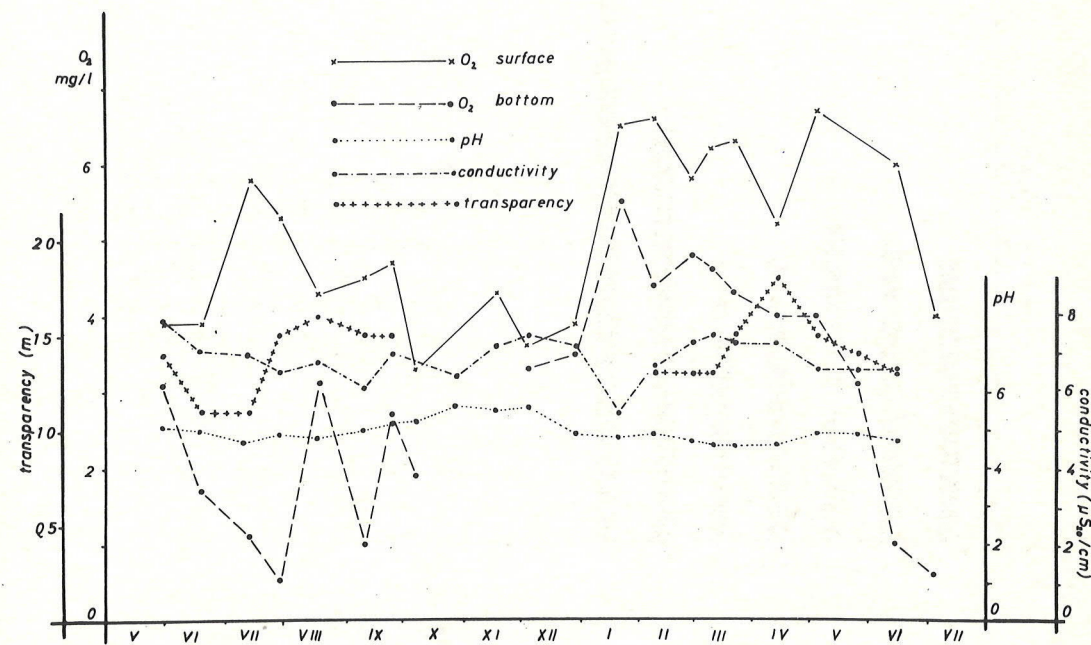


Fig. 38: Transparency, conductivity, pH, and oxygen concentration of station 7 at Rio Tarumã Mirim.

transparency seems to fluctuate periodically between 1 m and 1.5 m, according to the water level fluctuations. Color measurements during several years show considerable differences between different years (ANONYMUS 1972).

6.2.2. Conductivity

Many reports were published concerning the poverty of the black waters (SIOLI 1956 b, 1964, 1968 a, 1968 b, GESSNER 1960 a, 1960 b, 1964). Recent comprehensive investigations in the Rio Negro were made by H. UNGEMACH in the years 1966-1968 (ANONYMUS 1972). These analyses show the poverty of dissolved salts, particularly, of Ca^{2+} , being clearly a limiting factor for the mollusc community. The smaller affluents in the area of Manaus have a similar water chemistry (SCHMIDT 1972 a, MENEZES SANTOS et al. 1971). Thus, in the inundation forest at the Rio Tarumã Mirim only low conductivity values between 6 and $8 \mu\text{S}_{20}/\text{cm}$ were obtained (Fig. 38).

During rising water, a stratification of the conductivity occurs. The conductivity at the soil surface increases successively from deeper waters to the shoreline (Fig. 39), which may be caused by leaching of the substances decomposed during the dry period. It may be assumed, therefore, that a high percentage of nutrients of the terrestrial phase is released into the water.

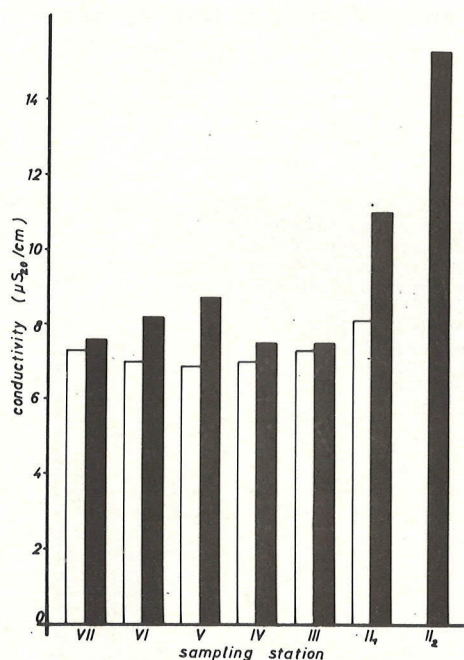


Fig. 39: Conductivity of bottom (white) and surface (black) water of the transect on 13-4-1972 at Rio Tarumã Mirim (II_1 = conductivity of station II at 0.5m water level, II_2 = directly on the shoreline).

6.2.3. Oxygen

The oxygen concentration shows a periodicity which may be correlated to the water level fluctuations. While the oxygen concentration at the water surface fluctuates between $\pm 4 \text{ mg/l O}_2$ and 7 mg/l O_2 , in the deep water a strong oxygen consumption was measured during the high water phase. The high values at the beginning of inundation between 4 mg/l O_2 and 6 mg/l O_2 decrease in June/July to 0.5 mg/l O_2 (Fig. 38) and remain in a more or less stable stratification (see chapter 6.2.4.). During the more rapidly falling water this stratification is destroyed. This process leads again to oxygen rich water. GESSNER (1961) re-

ferred to the oxygen stratification and explained the oxygen consumption in the deep water by the breakdown of the organic matter in the forest. The oxygen and temperature values of a transect show more clearly the stratification. On 10-9-71, at falling water, the level between the two layers lay at about 2 m (Fig. 40). The slight increase in the oxygen concentration of the deep water at station 7 (Fig. 40) may be due to current conditions of the Rio Tarumã Mirim.

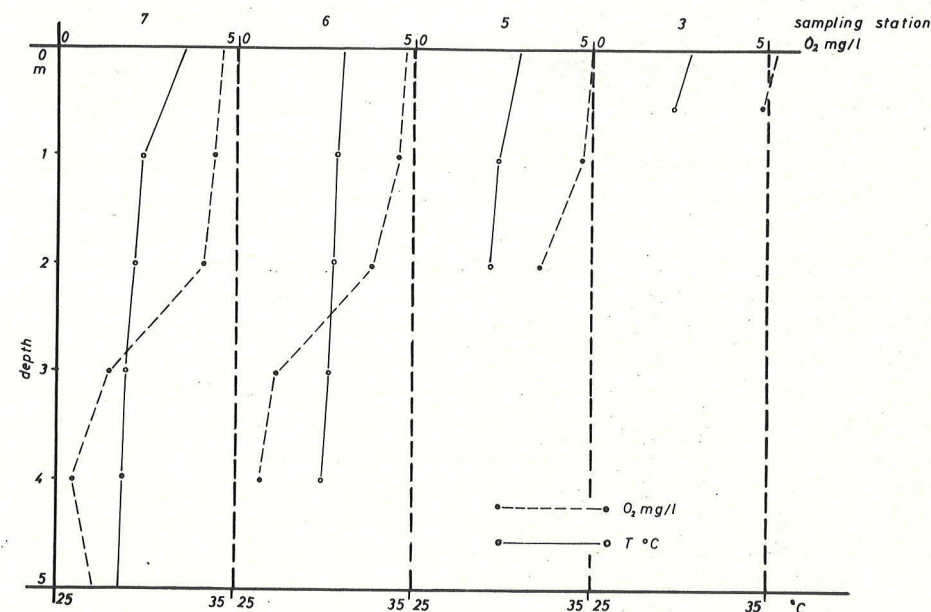


Fig. 40: Stratification of oxygen and temperature of station 3-7 on 10-9-71 at Rio Tarumã Mirim.

The following seasons can be determined:

1. beginning rising water: inflow of oxygen rich water;
2. rising water: beginning of the oxygen consumption in the deep water; (Till the end of May the oxygen concentration, in all parts of the forest, lies above 1 mg/l O_2 .)
3. high water and falling water: strong oxygen deficit in the deep water; oxygen concentration below 1 mg/l O_2 .

6.2.4. pH and temperature

Measurements of the temperature and pH show no periodicity of these environmental factors. The pH lies relatively constant between 4 and 5 (Fig. 38). The temperature fluctuates at the water surface at station 7 between 28°C and 32°C , and in the deep water between 27°C and 29.5°C .

Consequently, the temperature stratification was not very stable. At the time of strong oxygen stratification, often a temperature drop of only 1°C occurs. Density differences are greater at high temperatures than at equal thermal differences of lower temperatures and may cause stable stratifications. Nevertheless, the stability could not be very dis-

ting, because the thermal difference was very low and the thermoclin was shallow. In a forest, however, the influence of the wind is negligible, thus very labile stratifications may persist a longer time.

6.3. The macroinvertebrates of the benthos

6.3.1. The seasonal periodicity in the community composition

In the inundation forest at the Rio Tarumã Mirim the major part of the fauna is formed by the Náididae. They represent 27 % of the annual biomass and 78 % of the annual abundance. Furthermore, the chironomids occur with a relatively high biomass and abundance. *Euryrhynchus burchelli* CALMAN has a high percentage of the biomass, about 36 %, but is less abundant. Table 6 shows the species or animal groups found in the forest. The most important species are those of the Náididae, with at least 3 species. Furthermore the crustacean *Euryrhynchus burchelli* and the chironomid *Chironomus latistylus* are notable.

A distinct periodicity, as was found in the two other inundation forests, could not be found for the Rio Tarumã Mirim. Nevertheless, different seasons can be distinguished. Many species may be regarded as characteristic forest animals, because they only occur during the high water phase (Fig. 41). In the low water period they are wanting or in low abundances. During the high water period they show nearly no periodicity, however, they are highly abundant at the highest water level. To these species or animal groups belong: *aff. Naïs*, *aff. Dero* (Oligochaeta, Náididae), *Euryrhynchus burchelli* (Crustacea, Plaemonidae) and Ostracoda. Other animals, like Gomphidae (Odonata, Anisoptera) and *Tanytarsus* (Diptera, Chironomidae) are obviously restricted to the low water period. They were found in the forest only, because an extraordinary high low-water exists in the year of the research. The following phases in the community composition can be differentiated:

1. low water: Gomphidae, *Tanytarsus*, *Gundlachia bakeri*;
2. rising water: Náididae, Tubificidae, *Chironomus latistylus*, *Chir. sp. AR 4*, *Brasilocaenis irmieri*, Ostracoda, *Euryrhynchus burchelli*, Chaoboridae;
3. high water - falling water: Náididae, *Euryrhynchus burchelli*, Ostracoda, Chaoboridae, *Gundlachia bakeri*, *Polypedilum*.

6.3.2. The vertical stratification of the fauna

In contrast to the uniform seasonal periodicity, a distinct vertical stratification was detected (Fig. 42 and 43), particularly, for *aff. Naïs* and *Polypedilum* at falling water. At rising water *aff. Naïs* is more or less homogeneously distributed within all parts of the forest (Fig. 42). At the time of the highest water level its abundance at the lower flooded stations increased reaching its maximum abundance at station 1, while it disappeared nearly completely in the deeper lying area. At falling water short increases of abundance occurred successively at the stations each lying deeper than the preceding and being nearly vacant before. *Aff. Dero* shows a similar distribution in lower abundance.

The successive migration of the maximum abundance from higher lying stations to deeper lying stations can also be observed for *Polypedilum* (Fig. 43). This chironomid, however, is not obtained during the rising water.

Furthermore, the maximum abundance of the Náididae occurs at a water level of

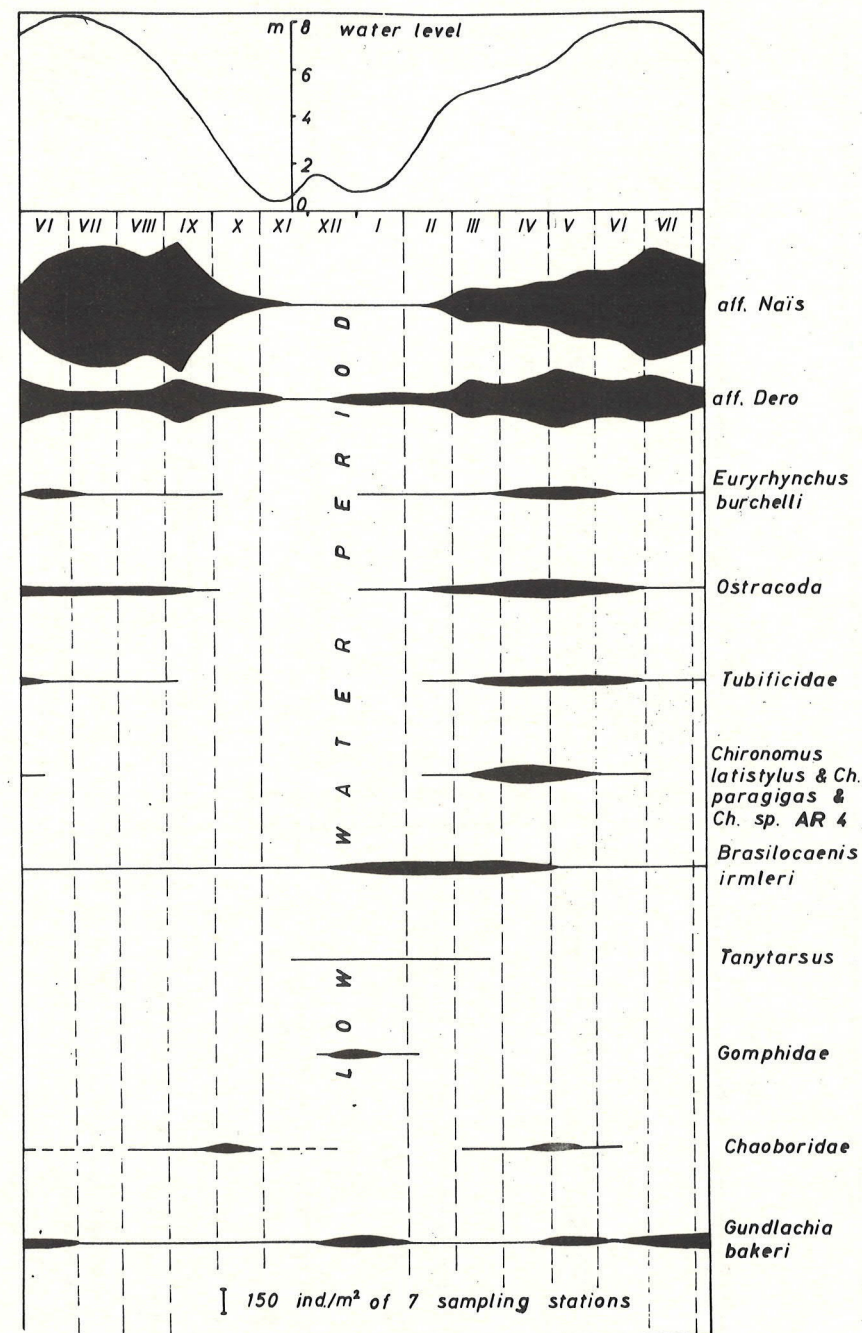


Fig. 41: The annual distribution of different species or animal groups compared with the water level fluctuations at Rio Tarumã Mirim.

Fig. 42: Distribution of *aff. Nais* and *aff. Dero* at Rio Tarumã Mirim

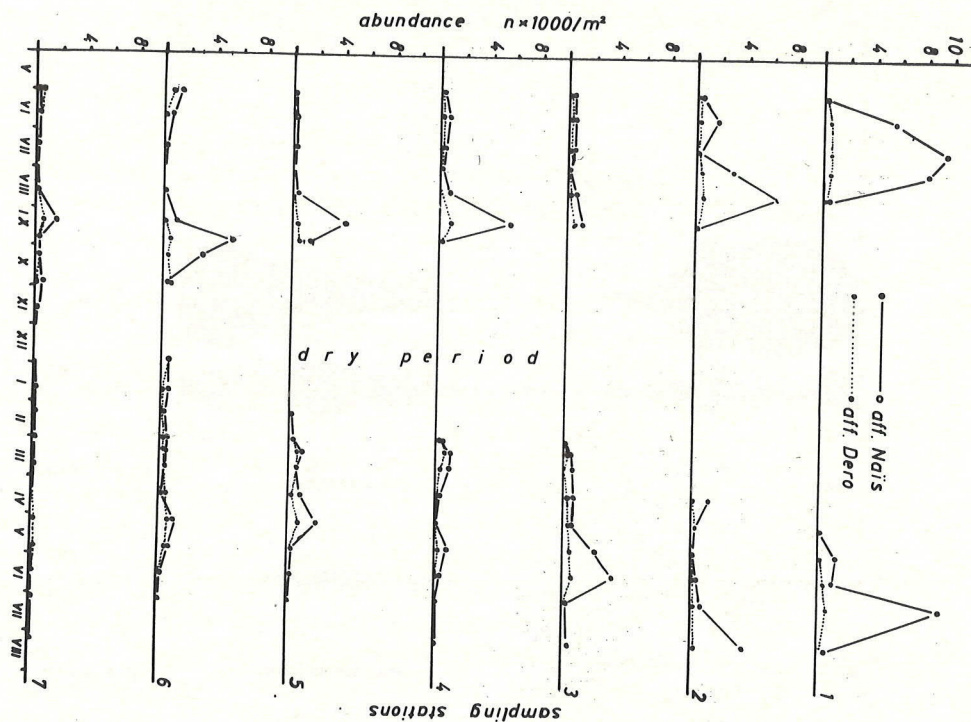


Fig. 43: Distribution of Tubificidae, Polypedium, Brasilocaenis irmleri PUTHZ, and the three Chironomus species at Rio Tarumã Mirim

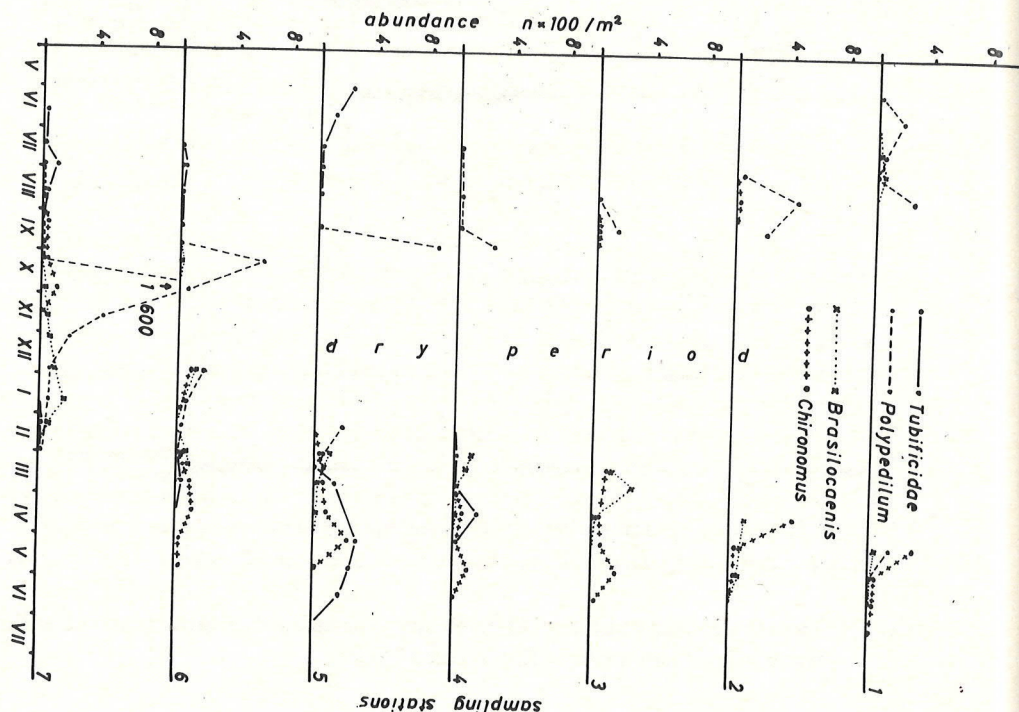


Table 6: The differentiated taxa of the inundation forest at Rio Tarumã Mirim (A - % of annual mean abundance, B - % of annual mean biomass).

taxonomic group	%A	%B	taxonomic group	%A	%B
NEMATHELMINTHES			Insecta		
Nematoda			DIPTERA		
			Chironomidae	8.9	10.0
PLATHELMINTHES			Chironomus latistylus REISS		
Turbellaria	2.0	1.8	Chironomus paragigas REISS		
			Chironomus sp. AR 4		
MOLLUSCA			Stenochironomus		
Gastropoda	1.6	3.7	Polypedium		
Gundlachia bakeri PILSBRY			further Chironomini species		
Uncancylus cf. barilensis			Tanytarsini		
MORICAND			Tanypodinae		
Ampullarius papyraceus			Orthoclaudiinae		
ANNELIDAE			Culicidae		
Oligochaeta	78.1	27.0	Chaoboridae		
aff. Nais			Ceratopogonidae		
aff. Dero			TRICHOPTERA	0.2	0.8
aff. Aulophorus			HETEROPTERA		
Opisthocysta flagellum LEIDY			Tenagobia socialis WHITE		
Tubificidae			ODONATA	0.2	12.7
Hirudinea			Zygoptera		
			Anisoptera		
ARTHROPODA			COLEOPTERA		
Acari	2.4	1.1	Helodidae		
Koenikea furcaticornis VIETS			Dytiscidae		
Frontipoda trispinosa LUNDBLAD			Gyrinidae		
Arrenurus taurus VIETS			Hydrophilidae		
Arrenurus angulosus VIETS			EPHEMEROPTERA	1.6	2.6
Arrenurus formosus VIETS			Asthenopus amazonicus HAGEN		
Crustacea			Brasilocaenis irmleri PUTHZ		
OSTRACODA	2.9	1.3			
DECAPODA	0.6	36.2			
Euryrhynchus burchelli CALMAN					

about 1.5-2.0 m, whereas *Polypedium* is found at a lower level of about 0.5-1.0 m.

Brasilocaenis irmleri and *Chironomus*, inhabiting the ground of the forest during rising water, start their production in the deeper lying area. They follow the rising water into the higher lying areas. The Tubificidae, inhabiting only the stations 4-7, seem to prefer a particular part of the forest.

It may be stated, that only few animals are restricted to a particular part of the forest. The major part of the fauna finds favourable living conditions in each part of the forest, if oxygen is available (see chapter 6.3.3.).

The maximum abundance of several animals at successive stations is chronologically correlated to the falling water. It seems improbable, that these animals form successive maximum abundances within a fortnight. The successive maximum abundances may be explained more easily by a translocation of the animals. That means that the Naididae and *Polypedium*, being very rapid animals, retreat with falling water. It could not be decided,

if the animals at rising water migrate into the forest with the water. Even in cultures with litter of the forest and rainwater no animal could be obtained. This experiment, however, was no solution, because the particular living conditions which must be established in the culture are unknown for the mentioned animals.

No sexual reproduction of the Naididae could be observed, whereas budding was always found. Therefore it can be assumed, that the few animals of the low water period on the shoreline affect a rapid reproduction during rising water by budding and an equal rapid inhabitation of the new living area.

Euryrhynchus burchelli is another instance showing the new inhabitation of the regained aquatic habitat (Fig. 44). During the low water period only few specimens exist,

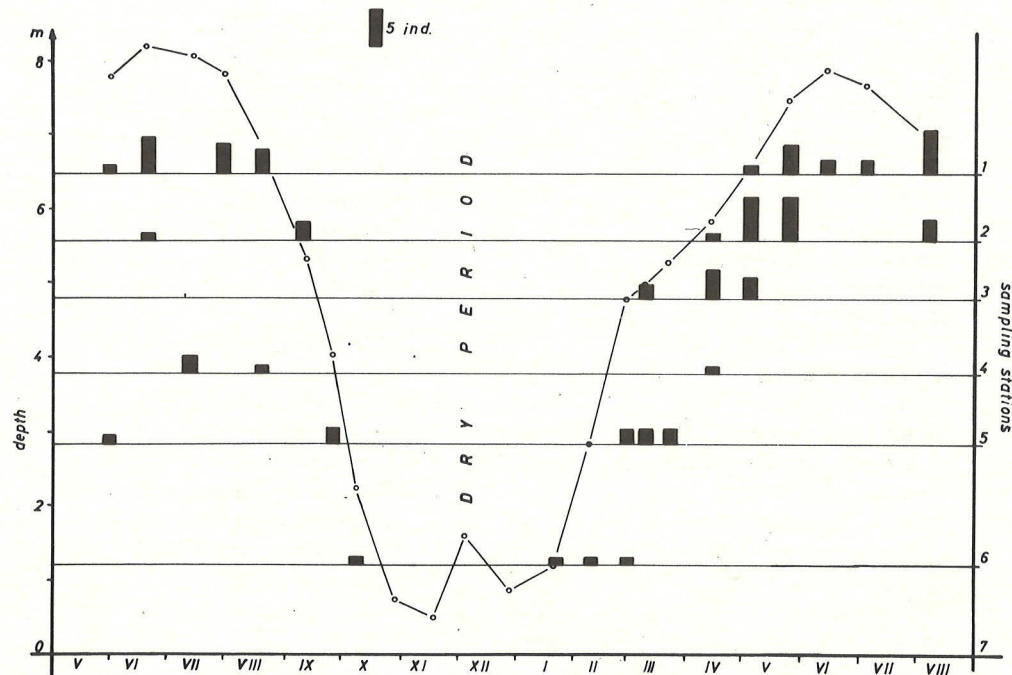


Fig. 44 : Distribution of *Euryrhynchus burchelli* CALMAN compared with the water level fluctuation at Rio Tarumã Mirim (the abundance/column refer to 3 samples).

which could not be obtained by sampling. During the rising water the prawn migrates with increasing abundance, in the proximity of the shoreline, into the forest. At the highest water level it could be obtained only at the highest station 1. During falling water a retreat was observed. The prawn, also, shows a migration in form of a translocation.

6.3.3. The most important factors for the periodicity and the stratification of the fauna

In spite of the high water level fluctuation, most of the environmental factors show

no periodicity excluding the distribution of the oxygen concentration within the several parts of the forest. It may be assumed, that this factor is of eminent importance for the benthos community. Since oxygen is nearly wanting during the second part of the inundation in the deep water, it may cause the absence of the fauna in this area (Fig. 42 and 43).

Indeed, on 10-9-71 a relationship between the abundance of the Naididae and the oxygen concentration was obtained (Fig. 45). Near the shoreline, however, a second mini-

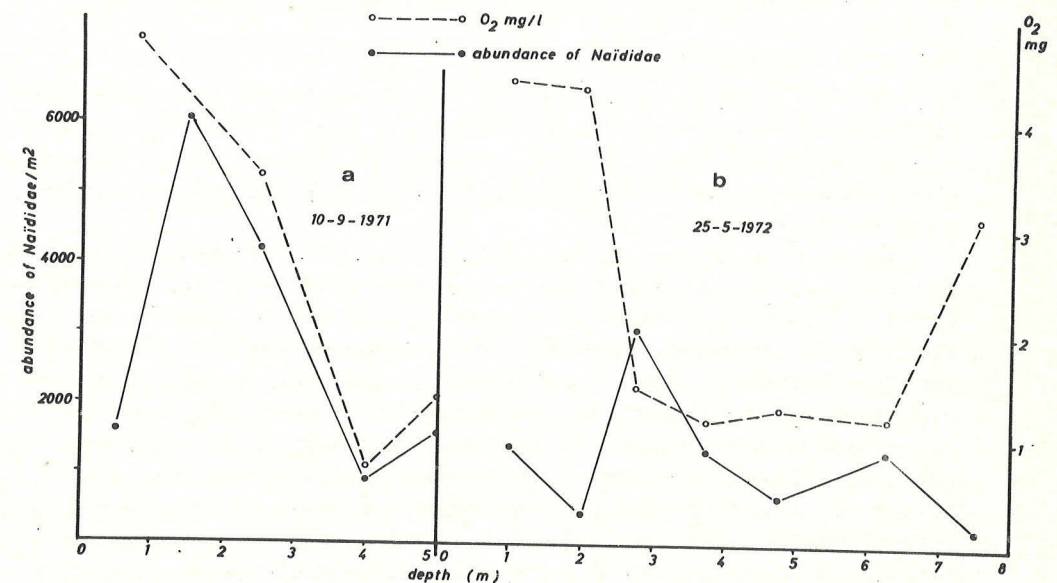


Fig. 45 : Abundances of Naididae compared with the oxygen concentration of the bottom water on 10-9-71 and 25-5-72 at Rio Tarumã Mirim.

mum population density existed. In the proximity of the shoreline a further limiting factor for the Naididae must be assumed. Because the mentioned distribution was found during the falling water, the retreat in front of the water may explain this phenomenon. The danger to remain on the dry land during the rapidly falling water may be too great, if they live nearer to the shoreline at this time.

On 25-5-72 no distinct correlation between the abundance of the Naididae and the oxygen concentration could be obtained (Fig. 45). It attracts attention, that on 25-5-72 the oxygen concentration lay at least above 1 mg/l O_2 , while at 10-9-71 at station 6 only 0.7 mg/l O_2 and at station 7 1 mg/l O_2 was measured. Already the investigations at Lago Janauari showed the value of 1 mg/l O_2 ($\pm 10\%$ saturation) being probably the critical tension for the Naididae and related species.

In the lakes of eastern Java the same limit value of 1 mg/l O_2 was found (RUTTNER 1952). There this limit value attracted attention by the stratification of the zooplankton.

GEISLER (1969) also mentioned, that Amazonian fish require at least 0.75-1.0 mg/l O₂. RUTTNER (1952) explained this relatively high limiting value with the dependance of the respiration on temperature, because the respiratory quotient of 1 mg/l O₂ at 25°C is only 1/5 of that at 5°C.

The different optimum areas of the species concerned in relation to the oxygen concentration may explain the distribution, immigration and emigration, in the different parts of the forest. Furthermore, at the retreat, the flight distance to the shoreline, being different for different species like Naïdidae and *Polypedilum*, must be considered.

6.3.4. Population dynamics

For the Naïdidae no sexual reproduction and the development of a clitellum could be observed. Budding, however, was regularly found.

Sexual ripe individuals of the South-American *Dero evelinae* MARCUS regenerate the middle and posterior part within eight days (MARCUS 1943). The gill-bearing respiratory organ was regenerated in 24 hours.

Further investigations of the population-dynamics of *Euryrhynchus burchelli* detect, that adult as well as young individuals occur during the whole year. This indicates, that no distinct generations but a continuous reproduction can be assumed for this prawn. Since the water level fluctuations are compensated by these vagrant animals, their influence on the population-dynamics may be less important. The heaviest found animal had a weight of 34.3 mg, the lightest 0.3 mg. The mean egg number/female was ± 15 eggs/ind.

It attracts attention, that at Rio Tarumã Mirim no species with a periodically constant generation cycle could be found like in the both preceding inundation forests. This fact may depend on the invariable environmental factors. Also the fluctuation of the oxygen concentration cannot induce a periodicity of distinct generations, because the animals retreat out of oxygen free areas. Thus, the species concerned were not forced to adapt their life cycles to the environmental conditions, which remain relatively constant during the course of a year.

6.3.5. Feeding habits

As is shown by the diet a greater part of the benthos fauna can be regarded as fungivores. Particularly, the Naïdidae feed on fungi. Leaf fragments were in the intestinal content of *Chironomus* and the leaf miner *Stenochironomus*, which are in low abundance. Therefore the percentage of the primary decomposers may be low. The result of the intestinal content study indicates, that the fungi are probably the most important decomposers in this inundation forest (Table 7) (see chapter 7.2.). Similar results were obtained by the investigations of the soil invertebrates (BECK 1971) and the study on soil fungi (STARK 1969) of the terra firme in the vicinity of Manaus.

In the inundation forests also the fish may play the role of primary decomposers. According to KNÖPPEL (1970) several fish species of Amazonian rivers prefer plant matter for their nourishment. The predators among the benthos community seem to feed particularly on the highly abundant Naïdidae (Fig. 15). Ostracoda and Chironomidae are less eaten.

A trophic system is obtained for the benthos community (Fig. 48). The basic source of food is given by the annual litter. In the terra firme rain forest an annual litter produc-

Table 7: The composition of the intestinal content of different taxa at Rio Tarumã Mirim

Detritivores	
Naïdidae and	
Opisthocystidae	: mainly fungi, less detritus and leaf fragments
Tubificidae	: fungi and detritus
Caenidae	: mainly fungi, less detritus and leaf fragments
Ancylidae	: mainly fungi, less detritus and leaf fragments
Chironomini	: mainly leaf fragments, sometimes numerous fragments of fungi
Predators	
Tanypodinae	: Naïdidae and Ostracoda
Anisoptera	: Naïdidae and Chironomidae
<i>Euryrhynchus burchelli</i>	: Naïdidae
Trichoptera	: Naïdidae

tion of 6.7-7.9 t/ha was obtained (KLINGE & RODRIGUES 1968). The dry weight of the litter in the inundation forest concerned amounts to 9-18 t/ha. Litter fall and litter breakdown are certainly influenced by the water level fluctuations (see chapter 7.2.). In the next level of this trophic system are the fungi and bacteria as primary decomposers. In lower percentages some soil invertebrates can be regarded as primary decomposers. The quantitative role of the fish on the breakdown is unknown. The major part of the benthos community, particularly, the Naïdidae, affects as secondary decomposers. These animals finally are the source of food for the predators among the benthos, the role of fish as predators has not yet been studied.

6.3.6. Productivity

Corresponding to the migrations of several animals, the biomass must fluctuate at the different parts of the forest. In the central forest two biomass maxima exist, one before the high water and one at the falling water (Fig. 17).

Because the sampling method only allows a rough quantitative estimation of the fauna some contradictions were obtained. The correct sampling was disturbed by the litter layer. Thus, the mean annual biomass of *Euryrhynchus burchelli* lies above that of the Naïdidae, certainly, because only a low percentage of the existing abundance could be obtained.

The highest biomass values occurred during the high water level at station 1, at the rising water at stations 3-4, and at the falling water at station 5 with ± 1 g/m². Regularly, the maximum biomass amounted to 0.3-0.8 g/m². The lowest biomass values were found at the highest water level in the oxygen poor areas of the central forest, where sometimes soil invertebrates were wanting. A further maximum occurred during the low water period near the shoreline, formed particularly by the Gomphidae.

The mean annual biomass of each station was 1 = 0.51 g/m², 2 = 0.25 g/m², 3 = 0.28 g/m², 4 = 0.19 g/m², 5 = 0.25 g/m², 6 = 0.3 g/m² and 7 = 0.16 g/m². In spite of all fluctuations of the soil invertebrate biomass in the central forest, the total biomass of the for-

est remained relatively constant during the inundation (Fig. 49). Also the annual biomass of each station is nearly the same. If the highest biomass of station 6 amounts to 100 %, that of station 1 = 89,6 %, 2 = 70,3 %, 3 = 91,6 %, 4 = 68,9 %, 5 = 97,4 %, and 7 = 86,6 %.

In respect to biomass calculations, both the total biomass of the forest and the biomass/m² must be regarded. The preceding values only give the biomass/unit area. In this inundation forest, where immigrations and emigrations are frequent, the calculation of the total biomass is important. For instance, if an area is reduced to half its extent, whereas the abundance of a given population remains equal, the population density is doubled. On the other hand the population density is halved, if the area extent is doubled. In this respect the biomass values per cent of the Naïdidae were calculated. The total biomass, that means the biomass of the area of the 7 stations and that of the variable area of only the flooded stations are compared to each other. Two parallel curves are obtained, which are shifted at appointed times (Fig. 46). The curve, biomass/total area, shows the production phases of

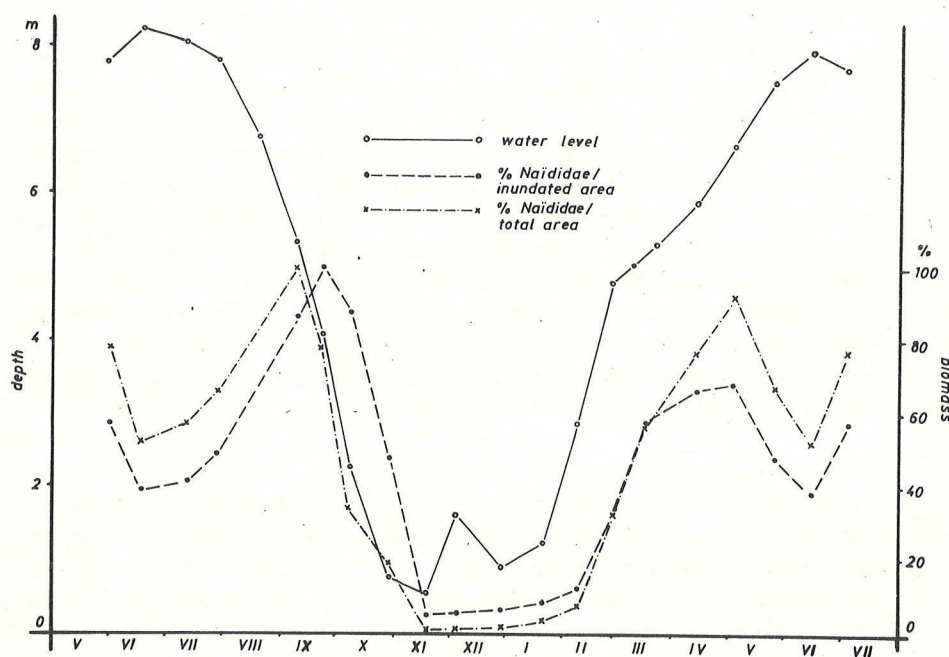


Fig. 46 : Biomass (% of the maximum biomass) of Naïdidae per inundated area compared with that per total area and the water level fluctuations at Rio Tarumã Mirim.

the animals more exactly, because the translocations are excluded in the calculation. In the curve, biomass/inundated area, the variable habitat extent is included in the calculation.

A comparison between the two curves has the following result. At the rising water the two curves are nearly identical. At this time, therefore, a homogeneous inhabitation of the expanding habitat can be assumed. In the following period the curve of the variable area extent lies below the other one. This may indicate, that the habitat expands more rapidly

than it can be inhabited by the increasing Naïdidae population. In the next period, the two curves are again shifted. At this time the habitat is reduced more rapidly than the Naïdidae population decreases.

No estimations could be made about the production in this inundation forest, because no generations could be differentiated or reproduction occurs by budding. It may be low, however, because the maximum biomass amounts only to 1 g/m².

7. Comparison of the three investigated inundation forests

7.1. Composition of the fauna

In the following part the relating and the differentiating facts between the three investigated inundation forests are studied. Whereas the annual, periodical water level fluctuations have relating effects, the influence of the different water bodies divides the three forests.

A comparison of the species composition shows euryecious species, which occur in each of the three inundation forests, as well as stenecious animals, which live only in one of the three inundation forests (Table 8). Additionally, numerous species exist which occur in mixed and black water or in mixed and white water. Particularly *Eupera simoni*, *Eupera bahiensis*, and *Laevapex aguadae* are links between white water and mixed water respectively *Asthenopus amazonicus*, *Gundlachia bakeri*, and *Euryrhynchus burchelli* between mixed water and black water. The published localities of *Euryrhynchus burchelli* indicate this species to live particularly in black waters but sometimes also in mixed waters (HOLT-HUIS 1966). On the other hand no species was found in white waters as well as black waters, avoiding the mixed water.

The differentiating factors may depend on the physical-chemical conditions of the different water bodies. In this respect the mixed water lies between the white water and the black water. This explains the relationship to the fauna of white waters as well as to black waters. Frequently, certain species show correlations to one of the numerous environmental factors caused by the different water types. For instance, the high sedimentation of the Amazon and the edaphic conditions connected therewith influence the distribution of *Campsurus notatus* and *Chironomus gigas*. On the other hand these conditions may be limiting for other species.

In black waters bivalves seem to be influenced less unfavourably by the pooriness of nutrients than by the low pH-value and the oxygen deficit. In a stress test with *Eupera simoni* in dest.-water, 10 $\mu\text{S}_{20}/\text{cm}$, 30 $\mu\text{S}_{20}/\text{cm}$, and 50 $\mu\text{S}_{20}/\text{cm}$ a lethal effect was only observed for dest.-water. How the electrolyte concentration influences the development of the young animals remains problematic. A lack of Ca^{2+} and the low pH may be limiting factors for the distribution of molluscs in black waters.

The species diversity of the macrobenthos is estimated to be about 100 species in the inundation forests. This species diversity seems to be relatively low. In the community of soil invertebrates in a terra firme rain forest 100-130 species were estimated only for Oribatei (Acari) (BECK 1971). ELTON (1973) found 38 taxa during 1 h 35 min in the lower field layer. BATES collected, during his journey of many years in Amazonia, 14 712 species (BATES 1863). In aquatic biocoenoses the numbers of species are also extraordinarily high. The chironomid fauna of the tropical South-America may contain 1000 species (FITTKAU 1971 a). Comparatively the low number of aquatic species in the inundation forest is astonishing. Also the number of terrestrial mite species, amounting to 75-90 spe-

Table 8 : Differentiated species or animal groups distributed on the three investigated inundation forests (++ frequently found, + found, - not found).

SPECIES	ILHA DE CURARI	LAGO JANAURI	RIO TARUMA MIRIM
<i>Campsurus notatus</i>	++	-	-
<i>Chironomus gigas</i>	++	-	-
<i>Pisidium sterkianum</i>	++	+	-
<i>Ampullarius sp.</i>	+	+	-
<i>Hebetancylus moricandi</i>	+	+	-
<i>Eupera simoni</i>	+	++	-
<i>Eupera bahiensis</i>	+	++	-
<i>Laevapex aguadae</i>	+	++	-
<i>Aroapyrgus sp.</i>	-	++	-
<i>Macrobrachium amazonicum</i>	-	+	-
<i>Ancylidae gen. sp.</i>	-	+	-
<i>Littoridina pusilla</i>	-	+	-
<i>Potamopyrgus latus</i>	-	+	-
<i>Tenagobia socialis</i>	-	+	+
<i>Asthenopus amazonicus</i>	-	+	+
<i>Gundlachia bakeri</i>	-	+	++
<i>Euryrhynchus burchelli</i>	-	+	++
<i>aff. Nais</i>	-	-	++
<i>Uncancylus c.f. barilensis</i>	-	-	+
<i>Ampullarius papyraceus</i>	-	-	+
<i>Koenikea furcaticornis</i>	-	-	+
<i>Frontipoda trispinosa</i>	-	-	+
<i>Arrenurus taurus</i>	-	-	+
<i>Arrenurus angulosus</i>	-	-	+
<i>Arrenurus formusus</i>	-	-	+
<i>Chironomus paragigas</i>	-	-	+
<i>Brasilocaenis irmieri</i>	++	++	++
<i>Opisthocysta flagellum</i>	++	++	+
<i>Chironomus latistylus</i>	+	++	+
<i>Chironomus sp. AR 4</i>	+	+	+

cies, is obviously lower in the inundation forest than in the terra firme rain forest (BECK 1971). The low species diversity as well as the high dominance values of single species may depend on the particular ecological conditions in the inundation forest. Whereas in the inundation forest few animals are high abundant, investigations on the floristic composition of the terra firme rain forest show that the ten most abundant species only amount to 24-25 % of the total abundance (KLINGE & RODRIGUES 1968). According to the second ecological principle (THIENEMANN 1918) the mentioned facts indicate the inundation forest to have unfavourable living conditions compared with the terra firme rain forest. The most important limiting factors in this respect may be the annual inundation, high sedimentation and the oxygen deficit of the deep water.

The environmental conditions in the inundation forest are induced by rapid changing of seasons within one inundation period. A distinct annual periodicity was found in the

three investigated forests, depending on the annual water level fluctuations and the environmental conditions connected therewith. As was described in the preceding chapters, both the inflowing water and several environmental factors, which are induced directly by the chemical and physical conditions of the different water types, cause a seasonal changing of the habitat. In white water areas particularly the sedimentation ratio, in black waters the oxygen deficit induce this periodicity. In each forest the inundation period can be subdivided clearly in three phases : rising water, high water, and falling water.

For the stratification of the benthos community also general principles could be detected. The different parts of an inundation forest are influenced by the differing duration of inundation during the year. Some parts of the higher lying forest are not inundated each year. By the water level measurements of 70 years at Manaus, an inundation rate of 31 % for a place being flooded 1 m in 1971 was calculated. Fig. 47 shows the inundation rate for

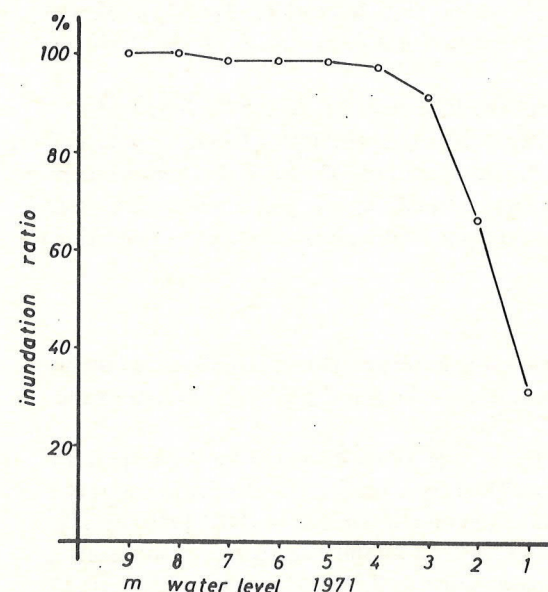


Fig. 47: Inundation ratio of sites inundated 1-9m in 1971.

forest parts of different altitude. A place, inundated 3-4 m during the research, is flooded by the water each year. In this respect each inundation forest can be subdivided in three parts: a higher lying area, being not inundated each year, with high terrestrial influence; a central part, being regularly inundated but lying still in the center of the forest; and at last a deeper lying area near the lake or the river, being at the border of the forest and influenced by both the forest and the free waters.

The parts near the border of the forest at the terra firme resp. the free waters can be differentiated by their different community composition like on Ilha de Curari and at the Lago Janauri. On the other hand it may have an effect on the abundance like at Lago Janauri and at the Rio Tarumã Mirim. The influence of the forest border on the benthos community differs according to the type of the inundation forest. It may be either favourable or unfavourable.

Some animals are adapted particularly to the living conditions in the inundation

forests. These animals have to be regarded as the characteristic fauna of inundation forests compared with those, which are immigrated from different limnic areas living only optionally in the inundation forest. In Amazonia adaptations to areas with seasonal change between water and dry land were found for fish (LÜLING 1969). Similar adaptations were detected in different tropical regions (McLACHLAN 1970) and in comparable habitats of the temperate zones (RUDESCU & BANU 1973, HESSE 1935).

Pisidium sterkianum, a species of the benthos community on Ilha de Curarí, is adapted to the inundation areas by its life cycle. It is not dependent directly on the forest habitat (see chapter 4.3.4.).

The high abundant *Eupera simoni*, however, depends on a good litter layer. This species developed the most remarkable adaptation to the inundation forest (see chapter 5.3.4.). Characteristic species of the inundation forest are also those which migrate according to the water level fluctuations but find optimal living conditions during the high water phase in the forest. Concerning this adaptations, Naididae, Opisthocystidae, *Euryrhynchus burchelli*, *Koenikea furcaticornis*, *Frontipoda trispinosa*, *Arrenurus taurus*, *A. angulosus*, and *A. formosus* have to be mentioned.

Furthermore, the adaptation by a rapid development was found for *Brasilocaenis irmieri* (see chapter 4.3.3.). This species may avoid the deteriorating habitats by developing a new generation in its favourable habitat. Other species like Culicidae and Ostracoda may be similarly adapted. A rapid transport of eggs or larval stages in just flooded areas causes an optimal development without competition from other animals, before the fast rising water changes the living conditions again.

7.2. Food chain

The investigated benthos community, living in forest habitats, is influenced by both the limnic and the forest environmental conditions. The forest obviously influences the edaphic and trophic conditions.

In waters the litter is attacked by different agents and prepared for decomposition. At first the water dissolves different matters. Then the chemical transformation starts by the breakdown of amino acids and other nitrogen containing matter (DÖLLING 1962).

The soil invertebrates are important by forming complex aggregates of inorganic matter with the mineral part of soil. They contribute to the transformation into humic substances.

According to the different trophic levels in the forest food chain, soil inhabiting animals can be subdivided into primary decomposers which feed directly on the litter and secondary decomposers, which feed on the feces of the precedings. Some animals may be regarded as primary as well as secondary decomposers like *Chironomus* (DÖLLING 1962). The development of soil invertebrates, involved in the litter breakdown, is influenced by the existing of primary decomposers (CUMMINS et al. 1973).

In forest habitats of temperate zones a high percentage of the soil invertebrates are primary decomposers. Also in aquatic biocoenosis numerous animals like *Asellus aquaticus*, caddisfly larvae, and Gastropoda were detected as primary decomposers (DÖLLING 1962, KAUSHIK & HYNES 1971).

In the terra firme rain forest, however, particularly fungi play the role of primary decomposers. BECK (1971) found that tropical animals, related to primary decomposers of

European forests, only have fungi fragments in their intestinal content. WENDT & STARK (1968) and STARK (1969) detected a direct nutrient cycling between the litter and the root system of trees by mycorrhizae. The predominant part of the soil invertebrates in the terra firme rain forest seems to play the role of secondary decomposers.

Comparing the feeding habits of animals found in the inundation forest with related European species, a higher percentage of fungivores is found in the tropical region. Ancyliidae, being deposit feeders of algae in European waters (SCHWENK & SCHWOERBEL 1973), feed on fungi periphyton in the litter of the inundation forest. The Naididae, *Dero*, being a leaf miner in Europe, also feeds on fungi. Some terrestrial animals of the inundation forest like Colobognatha and Glossoscolicidae were found to be facultative fungivores (SCHALLER 1973). On the other hand chironomids additionally feed on leaf fragments.

In the three investigated inundation forests the litter is of different importance for the animals. The litter amount differs in the three inundation forests. On Ilha de Curarí were 0-3.6 t/ha, at Lago Janauarí 5.4-9 t/ha, and at Rio Tarumã Mirim 9-18 t/ha. The litter is not the only source of food for the benthos community. Organic matter is transported by the current and serves as an important source of food. A general model of the food supply during the aquatic period in the inundation forest has to take into account both the litter and the organic material, imported into the forest from different limnic habitats (e.g. the floating meadows) (Fig. 48).

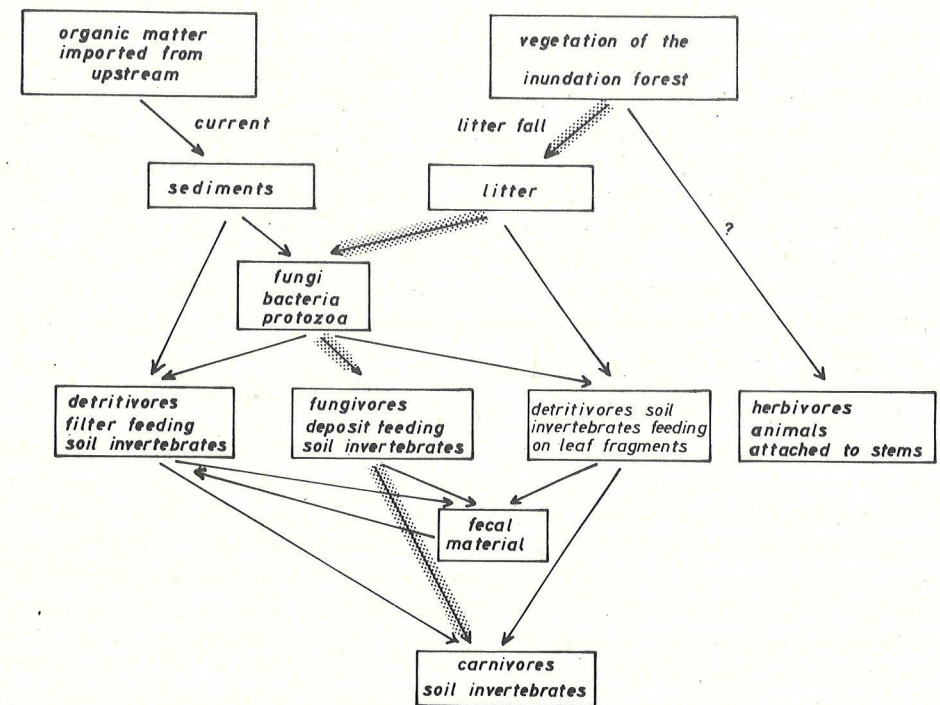


Fig. 48 : Food chain of the aquatic soil invertebrates of inundation forests. (The most important food chain of the inundation forest at Rio Tarumã Mirim is marked by the dotted arrows).

In addition to the different sources of food in the waters, the food supply has to be regarded. In lotic ecosystems the velocity of current, being 0.0-0.5 m/sec in the Rio Negro and 0.4-1.5 m/sec in the Rio Solimões, partly controls the food supply. If the same sources of food are supposed, an inundation forest at the Rio Solimões has a food supply three times higher than an inundation forest of the lower Rio Negro. In addition to the litter, in white and mixed waters the food supply by the current is of great importance for the filter-feeding bivalves (see chapter 5.3.5.). Bivalves, which often play a lower role in the food web of an ecosystem, may be important by the breakdown of organic material (TUDORANCEA 1972).

In the investigated black water inundation forest, filter-feeding species are wanting because the low velocity of current causes a small food supply. In this forest in particular deposit feeders are found. In white waters leaf decomposers, as well as the filter feeders, are important to the benthos community. Whether these species feed directly on the litter or if they feed on leaf fragments disintegrated by fungi, could not be determined. The increasing percentage of fungivores from white waters to black waters attracts attention. Herbivores could not be found in one of the three inundation forests. If microbes serve as a source of food for deposit feeders as well as filter feeders was not studied.

Not only the abundance of decomposers and the litter supply, but also the chemical conditions of the water influence the breakdown of the litter. Higher percentage of nitrogen and phosphorus in the water result in a faster breakdown (KAUSHIK & HYNES 1971). In addition, the oxygen supply of the deep water is important for the decomposition ratio. The higher oxygen deficit of the deep water at the Rio Tarumã Mirim impedes the breakdown, whereas in the investigated white and mixed water inundation forests always enough oxygen is available. The investigated inundation forests seem to differ due to their food chain and the decomposition ratio of the litter. The breakdown of the litter by fungi probably increases from white to black waters. Correspondingly, the food supply by allo-genic matter decreases. The most favourable trophic conditions occur therefore in the mixed water inundation forest. There a high supply of organic substances by the instreaming water and by the litter was found. Both filter feeders and deposit feeders find good living conditions. Furthermore, the environmental factors favour a rapid breakdown of the litter more than in black waters.

7.3. Productivity

In the composition of the fauna as well as in trophic and important environmental factors the inundation forest at Lago Janauari offers the most favourable living conditions of the three inundation forests. This may be seen also by the productivity values. The highest biomass values of $15.3 \times 4 \text{ g/m}^2$, at the end of the inundation at least $18.4 \times 4 \text{ g/m}^2$ in a short duration, are found in the forest at the Lago Janauari (Table 9). Correspondingly, the mean annual biomass of $3.0 \times 4 \text{ g/m}^2$ and the estimated production of $90-110 \text{ g/m}^2$ per year are the highest of the three forests. It must be regarded, that these values only refer to the aquatic phase.

Similar relationships were published for several aquatic habitats in Amazonia (FITT-KAU et al. 1975). The highest animal abundance and biomass occur in the floating meadows, amounting to a maximum abundance of $780\,000 \text{ n/m}^2$ and a maximum biomass of $11.6 \text{ g dry weight/m}^2$ (JUNK 1973). Comparatively, the values of lakes (REISS in FITT-KAU et al. 1975) seem to be very low. The biomass estimation in the inundation forest at

Table 9 : Comparison of productivity values between the three investigated inundation forests.

	Ilha de Curari	Lago Janauari	Rio Tarumã Mirim
$\mu\text{S}_{20}/\text{cm}$	27.3 - 54.2	13.7 - 65.7	5.4 - 7.5
mean annual abundance (n/m^2)	600	1300×4	1500
maximum abundance (n/m^2)	1600	5900×4	11 300
mean annual biomass (g/m^2)	1.2	3.0×4	0.2
maximum biomass (g/m^2)	4.0	$15.3 (18.4) \times 4$	1.1
estimated production ($\text{g/m}^2 \text{ Jahr}$)	$\pm 10 - 15$	$\pm 90 - 110$?

the Lago Janauari amounts to 12 g/m^2 , if the factor 4 is taken into account. Concerning the biomass, the investigated forests are within the range obtained for the floating meadows. Furthermore not only the soil was inhabited by the animals but also the flooded trees and shrubs. This substratum extraordinarily expands the living area for several animals. The part of the fauna living on trees and shrubs was not caught with the method used.

Comparing the annual periodicity of biomass between the three forests show further differences (Fig. 49). The biomass of the forest at the Rio Tarumã Mirim shows the most equable course. Only during the low water period was a maximum biomass obtained on the shoreline. This biomass course may be explained by the relatively uniform environmental conditions in black waters.

The biomass of the inundation forests at Lago Janauari and on Ilha de Curari fluctuate remarkably during the year. At the Lago Janauari the maximum biomass was obtained at high water, whereas on Ilha de Curari biomass values increase with falling water.

The dynamics can be explained by the ecology of the predominating species. *Eupera simoni* finds optimal living conditions at high water, whereas *Campsurus notatus* develops best at falling water on a thick sediment layer.

Fig. 50 shows the most important factors, which control the productivity in the inundation forest. The different chemical and physical conditions of the waters influence the properties of the habitat and the composition of the fauna. The annual fluctuation of several environmental factors controls the changing seasons.

The abundance in the total inundation forest depends on the duration of the inundation period and the extent of the living area. Furthermore, the food supply from limnic and terrestrial areas must be considered, differing according to the season and the altitude of the forest part. The adaptation, regarded as the most important biotic factor, make the

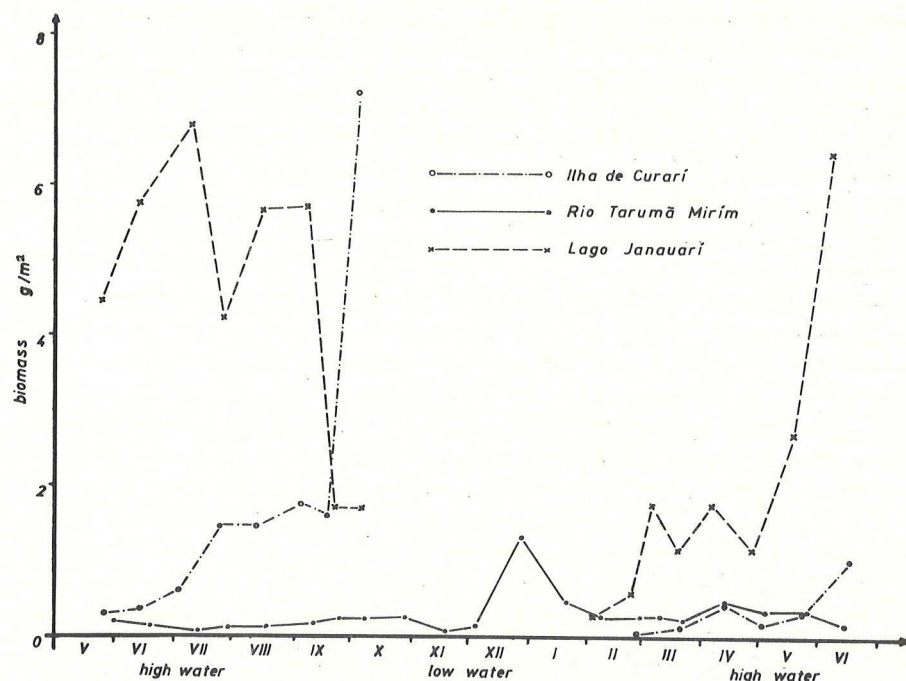


Fig. 49 : The periodicity of biomass in the three investigated inundation forests.

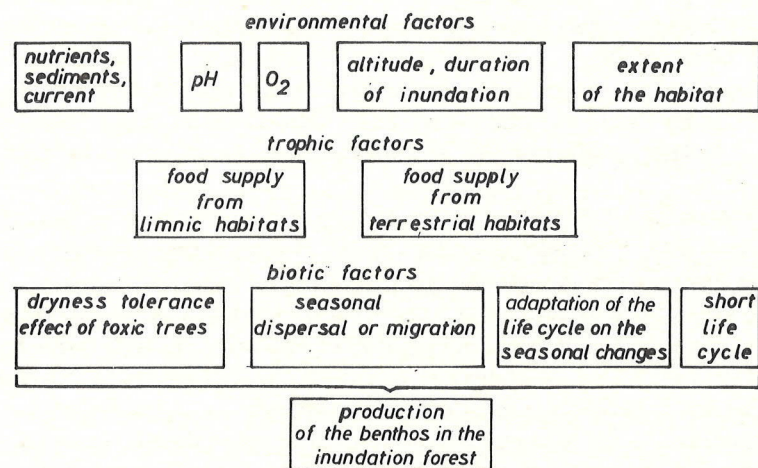


Fig. 50 : The most important factors influencing the productivity of inundation forests.

inundation forest, with its particular ecological conditions, available for the inhabitation of the fauna. Furthermore the toxicity of trees on nutrient-poor sites may have a huge effect on the litter fauna (JANZEN 1974).

In addition to the above mentioned factors, the terrestrial influence on the aquatic habitats has to be taken into account. Both fruits and insects falling from the trees on the water surface may serve as a source of food for fish. The inundation forest is an extraordinarily heterogeneous ecosystem with an innate complexity of limnic and terrestrial components differing during the changing seasons. Thus, the production can be comprehended only as the integral of all these components.

8. Summary

From January 1971 till August 1972 ecological studies were carried out on the aquatic macroinvertebrates of the benthos community of three Central-Amazonian inundation forests. The three investigated forests were chosen according to the influence of different water types. These forests were : 1. a site with an inflow of white water on Ilha de Curarí, 2. a site in a mixed water area at Lago Janauari, and 3. a site in a black water area at Rio Tarumã Mirim. The annual water level fluctuations caused similar ecological conditions concerning seasonal changes, whereas the differences between the forests depended on the inflow of the different water types.

The benthos composition differs according to the inundation forest type. Stenecious species, occurring only in one of the three forests, as well as euryecious species, inhabiting the three forests, were found. In addition many species were obtained which live either in white and mixed water or in mixed and black water.

The soil invertebrates adapted to the annual water level fluctuations. The most common adaptation may be seasonal dispersal, being developed as a migration or a translocation. Migrations could be detected for *Campsurus notatus* and *Eupera simoni* in white respectively mixed water. In black waters numerous species show a translocation, caused by the oxygen deficit of the deep water.

A diapause stage can be assumed for *Eupera simoni*. This dormant stage enables the bivalve to persist in the forest during the dry period.

Brasilocaenis irmieri presumably transports its eggs by the current in optimal habitats, where it develops rapidly in 14-21 days.

A dependence on the forest habitat was detected for some species of the mixed and black water. Other species of the inundation area, particularly of the white water area, are not dependent on the forest habitat.

In addition to seasonal changes in the benthos composition, a vertical stratification was found. The inundation forest can be subdivided in a river or lake near part, a central part, and a terra firme near part.

The intestinal content studies on the soil invertebrates and the oxygen conditions in the three inundation forests indicate the probable different breakdown of the litter in the forest of the várzea on the one hand and the igapó on the other hand.

Secondary productions could be estimated for the white water area with 10-15 g/m² and year and for the mixed water area with 90-110 g/m² and year. In the inundation forest of the mixed water, having the highest production of the three forests, environmental factors like oxygen concentration, sedimentation etc. and trophic factors offer favourable conditions for the inhabitation of the benthos.

9. Resumo

Estudos ecológicos foram efetuados de janeiro de 1971 a agosto de 1972 sobre os macroinvertebrados da comunidade bentônica de três tipos de floresta de inundação centroamazônicas. As três florestas estudadas foram escolhidas de acordo com a influência de diferentes tipos de água. Estas

florestas foram: 1. um local com um influxo de água branca na Ilha de Curarí, 2. um local em uma área de água mixta no Lago Janauarí, e 3. um local em uma área de água preta no Rio Tarumã Mirim. As flutuações anuais do nível d'água causaram condições ecológicas semelhantes devido às mudanças sazonais, enquanto as diferenças entre as florestas dependem do influxo dos diferentes tipos de água.

A composição do bentos difere de acordo com o tipo de floresta de inundação. Foram encontradas espécies estenóicas, ocorrendo apenas em uma das três florestas, assim como espécies eurióicas, habitando as três florestas. Além disso, muitas espécies coletadas vivem tanto em água branca e mixta, ou em água mixta e preta.

Os invertebrados do solo estão adaptados às flutuações anuais do nível d'água. A adaptação mais comum parece ser a dispersão sazonal, sob forma de uma migração ou uma translocação. Migrações puderam ser verificadas para *Campsurus notatus* e *Eupera simoni* em água branca respectivamente mixta. Em águas pretas numerosas espécies mostram uma translocação, causada pelo déficit de oxigênio da água profunda.

Um estado de diapausa pode ser assumido para *Eupera simoni*. Este estado dormente capacita o bivalvío a persistir na floresta durante o período de seca.

Brasilocaenis irmieri transporta provavelmente os seus ovos por meio da correnteza aos habitats ótimos, onde se desenvolve rapidamente em 14 a 21 dias.

A dependência do habitat florestal foi verificada para algumas espécies da água mixta e preta. Outras espécies da área de inundação, particularmente da área de água branca, não dependem do habitat florestal.

Ao lado das variações sazonais na composição bentônica foi encontrada uma estratificação vertical. A floresta de inundação pode ser subdividida em uma porção próxima ao rio ou lago, uma porção central, e uma porção próxima à terra firme.

Os estudos do conteúdo intestinal dos invertebrados do solo e as condições de oxigênio nas três florestas de inundação indicam as prováveis diferenças entre a degradação das folhas caídas na floresta da várzea de um lado e o igapó do outro.

Produções secundárias podem ser estimadas apenas para a área de água branca com 10-15 g/m² e ano, e para a área de água mixta com 90-110 g/m² e ano.

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